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Two new peacock spider species of the genus *Maratus* (Araneae: Salticidae: Salticinae) from south-western Australia

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ABSTRACT – The Australian endemic Peacock spider genus *Maratus* currently includes 97 species which are renowned for their elaborate courtship displays. Two new species are described from south-western Australia, *M. fletcheri* sp. nov. and *M. harveyi* sp. nov. Recently collected material has extended the range of *M. madelineae* Waldock, 2014. A brief summary of the courtship display for *M. fletcheri* sp. nov. is included.

KEYWORDS: taxonomy, morphology, south-western Western Australia

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INTRODUCTION

The jumping spider genus *Maratus* Karsch, 1878 is endemic to the Australian region, and currently includes 97 species and one subspecies (World Spider Catalog 2020). The males of most species of *Maratus* have brightly coloured abdomens, with lateral flaps or fringes of coloured setae that are inflated during courtship displays (e.g. Waldock, 2014; Otto & Hill 2017; Otto & Hill 2018). Males of many species also have enlarged, setose third legs, which are used in the complex display performance. Following recent field work in south-western Western Australia, members of the Project Maratus team (see https://www.facebook.com/projectmaratus/) collected an undescribed species, *M. fletcheri* sp. nov., and extended the known distribution for *M. madelineae* Waldock, 2014. An additional species, *M. harveyi* sp. nov. is also described here.

MATERIAL AND METHODS

The material examined for this study is lodged in the Western Australian Museum, Perth, Australia (WAM). Specimens were preserved and described in 75% or 95% ethanol, illuminated with Halogen lights, and illustrated with the abdomen and cephalothorax in a flat, horizontal position. Female genitalia were examined by dissecting epigynes from the abdomen and clearing them in 10% lactic acid at room temperature for several days. Epigynes were mounted in glycerol and illustrated with a camera lucida on a Leica DM 2500 compound microscope. Other drawings and measurements were made using a Leica MZ6 or Leica MZ16A stereo microscope and Leica Application Suite V3.8.0 from Leica Microsystems Ltd. Terminology for male and female genitalia follow Żabka (1987).

TAXONOMY

Family Salticidae Blackwall, 1841

Subfamily Salticinae Blackwall, 1841

Genus *Maratus* Karsch, 1878

Maratus Karsch, 1878: 27.

TYPE SPECIES

Maratus amabilis Karsch, 1878, by subsequent designation of Bonnet (1957: 2713).

COMPOSITION

Maratus is considered a member of the tribe Euophryni, subfamily Salticinae following Maddison (2015). As of November 2020, there were 97 named species and one subspecies of *Maratus* recognised (World Spider Catalogue 2020).

REMARKS

The species-specific (and often spectacular) colour patterns on male *Maratus* species are the result of specialised short squamous setae, which cover the dorsal abdominal scute and parts of the dorsal carapace (Figures 6, 15). These setae reflect different colours, depending on the angle of orientation and reflect different colour spectra on different parts of the abdomen (Figures 6, 15). When preserved in alcohol, the vibrancy of the colours may be reduced, e.g. squamous setae that appear red in life will show as orangey to light brown over time. To standardise the colour pattern descriptions, the specimens were viewed under Halogen lights with the abdomen and cephalothorax in a flat, horizontal position. This combination leads to the squamous setae reflecting colours as rose-gold, orangey, brown and pink. When the abdomen is raised to a vertical position the rose-gold squamous setae reflect as electric blue; in life these rose-gold coloured areas are blue/green. In addition, where available, digital images of live males of *M. fletcheri* sp. nov. and *M. harveyi* sp. nov. have been included.

***Maratus fletcheri* Waldock, sp. nov.**

Fletcher's Peacock Spider

Figures 1–9, 19

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MATERIAL EXAMINED

Holotype

Australia: ***Western Australia*:** ♂, c. 11 km NE. of Cowaramup on Jindong-Treeton Road, 33°48'35"S, 115°12'55"E, 18 September 2016, A. Fletcher, M. Doe, M. Duncan (WAM T140702).

Paratypes

Australia: ***Western Australia*:** 3 ♂, 3 ♀, Treeton, W. side of Smith Road, 33°48'36"S, 115°13'41"E, 17 September 2016, A. Fletcher, M. Doe, M. Duncan (WAM T146586–91).

DIAGNOSIS

Males of *Maratus fletcheri* may be distinguished from all other known species in the *Maratus vespa* species-group (Otto & Hill 2018) except *M. harveyi* sp. nov. by the absence of red patches or stripes in the centre of the optical region. In common with all other species in the *M. vespa* group, the abdominal pattern in males consists of two regions with distinctively different colouration and patterning: *M. fletcheri* resembles that of *M. vespa* Otto & Hill, 2016, *M. icarus* Otto & Hill, 2019a and *M. cristatus* Otto & Hill, 2017 by the presence of blue/green and red stripes in the anterior half of abdomen (Figure 6), but these stripes are arranged differently for each of these species and in *M. fletcheri* the red stripes continue as tan and black stripes on the posterior half. The third legs of *M. fletcheri*, which have dense brown and black brushes on all segments and white bristles in clumps on the femur, patella and tibia (Figures 3, 6), resemble *M. vespa*, but the brushes on the femur are brown instead of white (Figure 6).

Females of *M. fletcheri* differ from all other known *Maratus* species except *M. madelineae* Waldock, 2014 and *M. karrie* Waldock, 2013 by the swollen proximal receivers that abut at the median guide (Figures 8, 9), and by the enlarged intermediate canals abutting at the median guide. The fossae are laterally compressed compared to all other known *Maratus* species.

DESCRIPTION

Male (holotype)

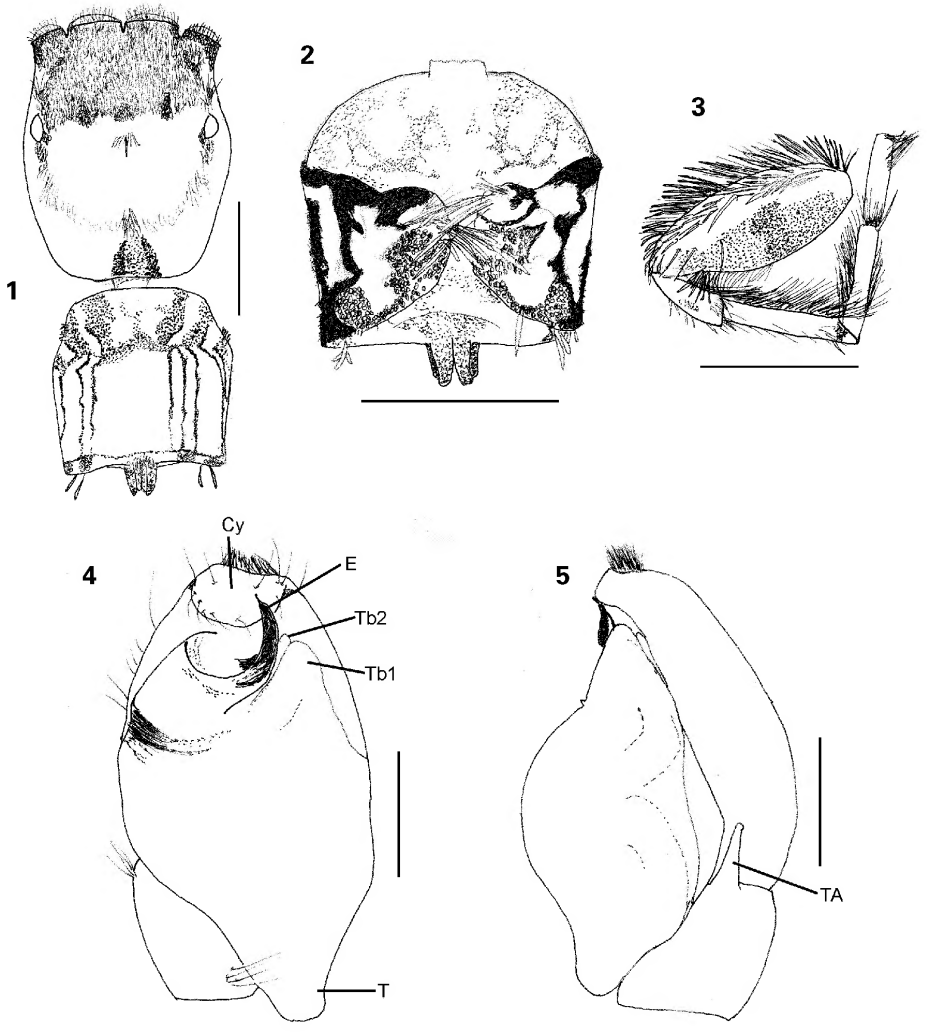
Cephalothorax black to dark brown with white setae bordering lateral edges. Dense mat of light pale blue squamous setae covering ocular region, small patches of orange setae posterior to ALE and adjacent to PLE; elongate orange patches of setae extending from posterior edge of ocular area towards AME; tuft of white setae between PME and PLE; oval patch of white setae posterior to fovea. Anterior eyes fringed with creamy setae along dorsal margin, ALE surrounded by orangey setae; rest of cephalothorax lightly covered with scattered short white setae and brown bristles (Figures 1, 6). Clypeus golden yellow, chelicerae dark brown, cream distally. Maxillae light cream, labium dark grey with cream edge. Sternum dark grey.

Venter of abdomen dark yellow with greyish smudges in centre and laterally; spinnerets dark grey. Dorsal abdominal scute developed as short lateral flaps which do not meet across the venter when relaxed; the lateral extensions exhibit a continuation of the posterior half of the dorsal pattern. Posterior half of dorsum with greyish squamous setae with lighter grey bands outlined with narrow lines of short black setae (Figures 1, 6). Anterior half of dorsal abdomen with red-orange squamous setae as six bands extending lengthwise to anterior edge, alternating with bands of greenish-blue squamous setae (Figures 1, 6) with black setae that continue as extensions of the anterior red bands; posterior edged with short black setae interspersed with small patches of greenish-blue squamous setae. Black and grey longitudinal bands continue onto lateral flaps with two circular patches of greyish squamous setae surrounded by short black/electric blue setae distally and plumose electric-blue setae along distal edge of flaps (Figure 2). Anterior corner of flap with very long dark grey and cream bristles; posterior border of flaps with short black squamous setae interspersed with orangey-red short squamous setae. Up to four long plumose black/electric blue iridescent setae spaced along posterior border of flaps (Figures 2, 6). Dorsal scute not covering spinnerets, this area lacking squamous setae and dark grey with short brown setae; creamy strip of

short setae merging with white patch at tip of abdomen (Figures 1, 6).

Legs I, II and IV: proximal femora cream dorso-anteriorly with dark grey patches ventro-posteriorly; patellae, tibiae, metatarsi and tarsi tan with grey bands at joints; covered with dense short white setae interspersed with black bristles. Leg III: dorsal femur cream, rest dark grey, patella tibia and metatarsus dark yellow with greyish patches at joints; tarsus cream. Femur, patella and tibia with thick brush of long setae dorso-ventrally; dorsal femur and patella with white brush setae; brush setae on tibia greyish, becoming creamy distally (Figures 3, 6); metatarsus with greyish brush setae ventrally; tarsus with thick short white setae on all surfaces and longer white setae at tip, covering claws (Figures 3, 6).

Pedipalp yellow with greyish patches on proximal segments. Tibial apophysis narrow, straight (Figure 5). Cymbium, dorsal tibia and dorsal patella densely covered with long creamy setae, a single very long black seta on dorsal pedipalpal patella; tibia and cymbium with a few long creamy and brown setae on ventral side just under tegulum. Embolus with broad tip and conductor closely aligned with embolus into tight coil,



FIGURES 1–5 *Maratus fletcheri* sp. nov., male holotype (WAM T40702): 1) cephalothorax and abdomen, dorsal view; 2) abdomen, ventral view (abdominal flaps folded); 3) left leg III, retrolateral view; 4) left pedipalp, ventral view; 5) left pedipalp, retrolateral view. Scale lines = 1 mm (Figures 1–3), 0.3 mm (Figures 4–5). Cy = cymbium; E = embolus; T = tegulum; TA = tibial apophysis; TB1–2 = tegular bulges 1–2.

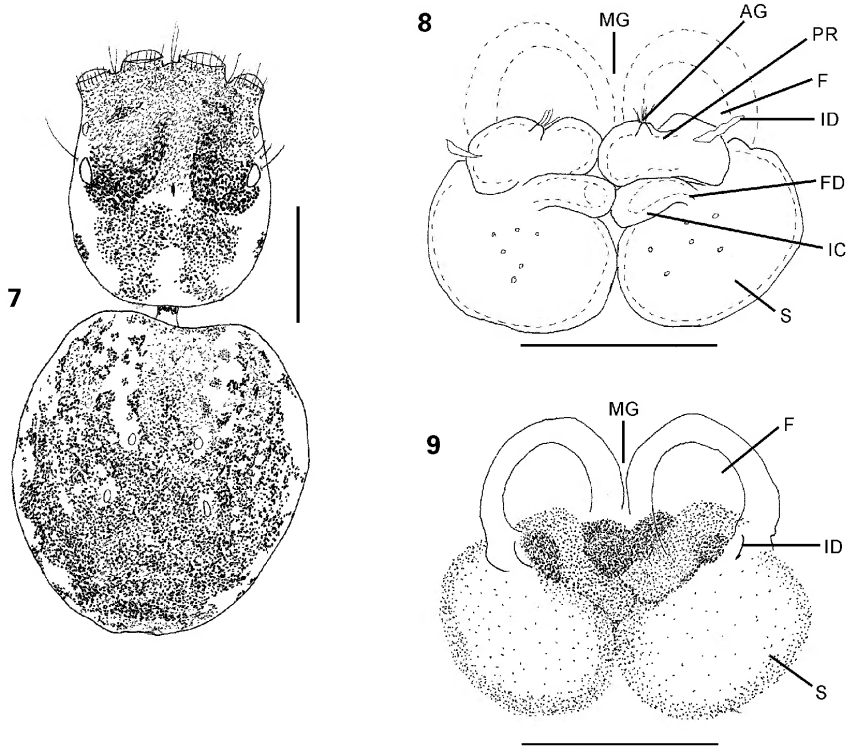
FIGURE 6 *Maratus fletcheri* sp. nov., photograph of male with extended abdominal flaps. (Image courtesy A. Fletcher.)

tucked under tip of cymbium; tegulum with two bulges adjacent to embolus (Figure 4).

Female (paratype, WAM T146591)

Ocular region black, densely covered with short creamy and black setae; black setae concentrated in area around PLE, extending towards centre and AME; rest of cephalothorax golden-yellow with grey to light grey patches and scattered creamy and black setae. Posterior to ocular area and fovea, yellow with broad grey patch posterior to fovea; two broad grey bands extend to posterior margin with yellow central strip (Figure 7). Sides of cephalothorax yellow with small light grey patches. Clypeus light yellow; chelicerae, maxillae, labium light yellow with white border. Sternum cream with light grey edging.

Abdomen oval with tan dorsal sigilla and black bristles scattered amongst brown and creamy setae; most of dorsum covered in dark grey to black diffuse pattern on creamy background; pattern darkens and narrows to point above spinnerets (Figure 7). Venter of abdomen cream, with small grey spots in longitudinal rows, larger



FIGURES 7–9 *Maratus fletcheri* sp. nov., female paratype (WAM T146591): 7) cephalothorax and abdomen, dorsal view; 8) cleared epigyne, dorsal view; 9) epigyne, ventral view. Scale lines = 1 mm (Figure 7), 0.25 mm (Figures 8–9). AG = accessory gland; F = fossa; FD = fertilisation duct; IC = intermediate canal; ID = insemination duct; MG = median guide; PR = proximal receiver; S = spermatheca.

elongate spots at edges. Ventral spinnerets cream, dorsal pair, dark grey.

Femora and patellae of legs yellow, no markings dorsally, grey patches at joints and mid-way of femora; tibiae, metatarsi and tarsi yellowy with grey bands at joints.

Proximal receivers of epigyne large and abutting each other at median guide. Openings of intermediate canals situated at centre of anterior margin of spermathecae, abutting at median guide. Insemination ducts opening on lower lateral border of fossa, over lateral coil of proximal receiver; fossae laterally compressed ovals (Figures 8–9).

Dimensions (mm)

Holotype ♂ (paratype ♀, WAM T146591): total length (excluding chelicerae) 3.60 (4.96). Carapace length 2.12 (2.13). Abdomen length 1.47 (2.64). Leg I: femur 0.95 (0.84), patella 0.63 (0.61), tibia 0.62 (0.56), metatarsus 0.43 (0.41), tarsus 0.35 (0.39). Leg II: femur 0.87 (0.88), patella 0.60 (0.52), tibia 0.55 (0.51), metatarsus 0.41 (0.47), tarsus 0.31 (0.38). Leg III: femur 1.37 (1.34), patella 0.53 (0.71), tibia 0.84 (0.82), metatarsus 0.66 (0.74), tarsus 0.55 (0.54). Leg IV: femur 0.98 (1.24), patella 0.43 (0.49), tibia 0.72 (0.63), metatarsus 0.72 (0.81), tarsus 0.46 (0.49). Legs, relative lengths: III: IV: I: II (III: IV: I: II).

DISTRIBUTION

Maratus fletcheri has only been recorded from near Treeton, south-western Australia (Figure 19), in *Banksia*, jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) woodland.

MATING BEHAVIOUR

Courtship behaviour has been observed for five male and female pairs (see https://www.youtube.com/watch?v=Ly3AYL7cktI by A. Fletcher, M. Duncan & M. Doe, accessed 30 November 2020). The male raises one or other third leg, which attracts the female's attention. Once the female is watching, the male raises the other third leg as well as raising and expanding the abdominal fan centrally. The fan is quickly shaken from side to side and lowered then raised and shaken again. Then the male rotates the fan to one side (closing the extended flap on the opposite side) and extends the plumose setae (elongated setae on the tip of the lateral flaps).

The female appears to be attracted to these elongate setae as they emerge at the side of the male vibrating at the tip of the extended lateral flap. The female's focus swaps from the left and right sides as the male 'hides' these setae behind the setose third legs. The male holds this pose for a short time and then changes sides, rotating the fan to the opposite side and revealing the plumose setae again, the female closely mirrors these changes from side to side as evidenced by movements of the cephalothorax. This behaviour is not unlike teasing a cat with a moving object. This 'teasing' will continue for up to three minutes with both the male and female moving forwards and backwards, closer and farther from each other.

ETYMOLOGY

The specific epithet is a patronym in honour of Adam Fletcher, photographer and collector, and founding member of Project Maratus.

***Maratus harveyi* Waldock, sp. nov.**

Harvey's Peacock Spider

Figures 10–18, 19

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MATERIAL EXAMINED

Holotype

Australia: ***Western Australia*:** ♂, Barrabup Road, W. of Nannup, 33°58'52.6"S, 115°44'58.0"E, 28 October 2018, C. O'Toole, P. Irvine (WAM T59140).

Paratypes

Australia: ***Western Australia*:** 1 ♂, Barrabup Road, NW. of Nannup, 33°58'53"S, 115°44'58"E, 21 October 2018, M.S. Harvey, M.E. Blosfelds (WAM T146690); 2 ♂, Barrabup Road, W. of Nannup, 33°58'52.6"S, 115°44'58.0"E, 28 October 2018, C. O'Toole, P. Irvine (WAM T59141, T59142); 1 ♀, Barrabup Road, W. of Nannup, 33°58'52.6"S, 115°44'58.0"E, 28 October 2018 (moulted to adult 30 November 2018), C. O'Toole, P. Irvine (WAM T59143).

DIAGNOSIS

Males of *Maratus harveyi* can be distinguished from all other known species in the *Maratus vespa* species-group (Otto & Hill, 2018) except *M. fletcheri* sp. nov., by the absence of red patches or stripes in the centre of the optical region of the cephalothorax. In common with all other species in the *M. vespa* group, the abdominal pattern in males consists of two regions with distinctively different colouration and patterning: while *M. harveyi* resembles *M. icarus* Otto & Hill, 2019a and *M. cristatus* Otto & Hill, 2017 by the presence of blue/green and red stripes in the anterior half of abdomen, *M. harveyi* differs as these stripes do not extend into the posterior half and there is a red band delimiting the pattern-less posterior half. The third legs of *M. harveyi* have dense light brown brushes on the femur, dense dark grey and black brushes on the patella, tibia and metatarsus, and white bristles in clumps on the patella and tibia (Figures 12, 15), resembling *M. vespa* Otto & Hill but with the brushes on the femur brown instead of white.

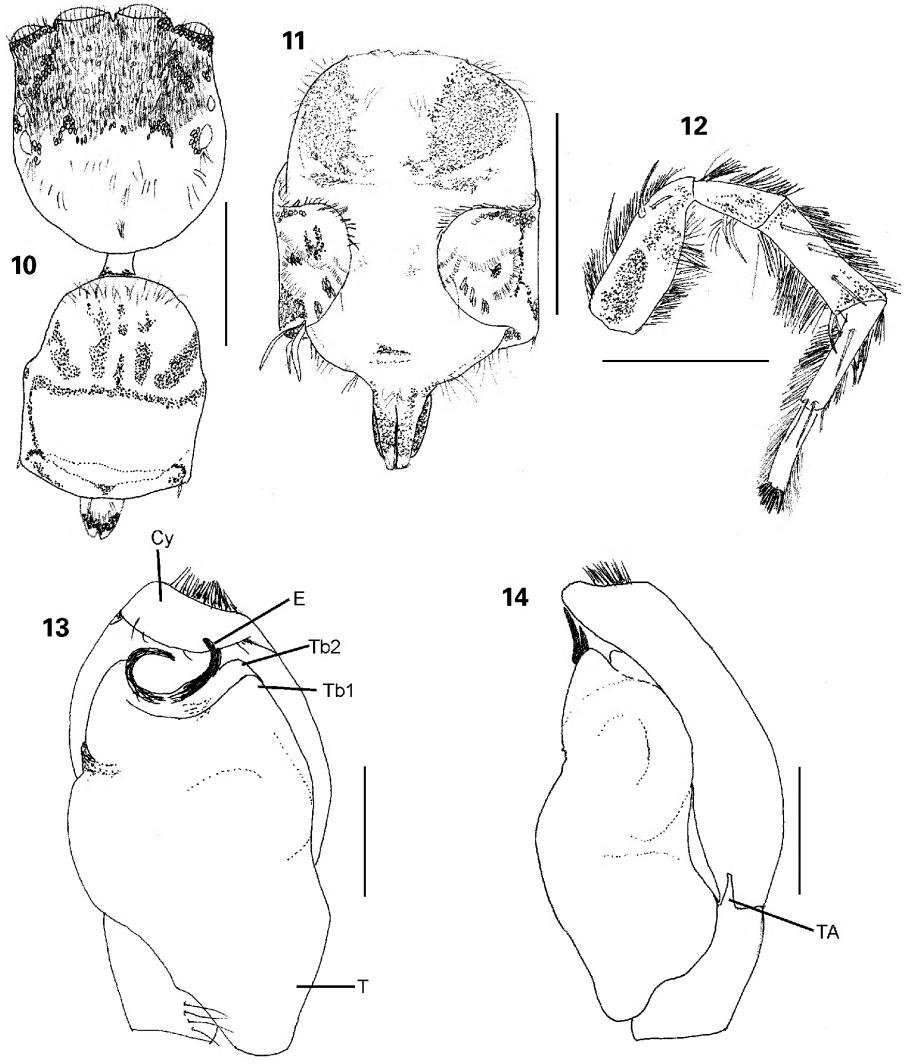
Females of *M. harveyi* differ from all other known *Maratus* species except *M. banyowla* Otto & Hill, 2019b and *M. sarahae* Waldock, 2013 by the tightly coiled proximal receivers that do not extend to the lateral borders of the fossae (Figures 17–18).

DESCRIPTION

Male (holotype)

Cephalothorax black to dark brown with white setae bordering lateral edges. Dense mat of off-white squamous setae covering ocular region with light orange patches posterior to ALE; patch of white setae posterior to fovea. ALE fringed with orangey setae along dorsal margin, AME fringed with off-white setae along dorsal margin; patch of white setae posterior to PME, rest of cephalothorax lightly covered with scattered short brown setae and dark brown bristles (Figure 10). Clypeus pale yellow, chelicerae dark grey to black. Maxillae yellowish, labium dark grey with cream edge. Sternum dark grey.

Venter of abdomen pale yellow to white posteriorly with sparse greyish smudges in centre and laterally; spinnerets dark grey (Figure 11). Posterior half of dorsal abdominal scute developed as lateral flaps that fold around the sides of the abdomen but do not overlap on the venter; flaps exhibit a continuation of dorsal pattern (Figures 11, 15). Anterior half of dorsal abdomen with



FIGURES 10–14 *Maratus harveyi* sp. nov. male holotype (WAM T59140): 10) cephalothorax and abdomen, dorsal view; 11) abdomen, ventral view (abdominal flaps folded); 12) left leg III, retrolateral view; 13) left pedipalp, ventral view; 14) left pedipalp, retrolateral view. Scale lines = 1 mm (Figures 10–12), 0.3 mm (Figures 13–14). Cy = cymbium; E = embolus; T = tegulum; TA = tibial apophysis; TB1–2 = tegular bulges 1–2.

red-orange squamous setae as three central longitudinal bands and two oblique bands extending to anterior edge (five bands in total) with a narrow continuous stripe across dorsum extending onto lateral flaps; blue-green squamous setae between bands (Figures 10, 15). Posterior half of dorsum grey, covered with very short squamous setae; with creamy crescent along posterior border, also covered with very short squamous setae; posterior edge of scute with border of alternating orange and blue-green squamous setae patches and scattered black squamous setae; several long plumose black/electric-blue setae on each side of the postero-lateral edge of the flap (Figures 11, 15). Central white patch of setae above spinnerets (Figures 10, 15). Lateral flaps with purplish-blue 'eye' patch; border of short black squamous setae. Orange band from dorsum does not extend onto flap but follows main part of flap. Narrow border of orangey short squamous setae on anterior edge of flap; remainder of flap with grey and black/electric-blue short squamous setae; black/electric-blue setae particularly dense along border of flap (Figure 11).

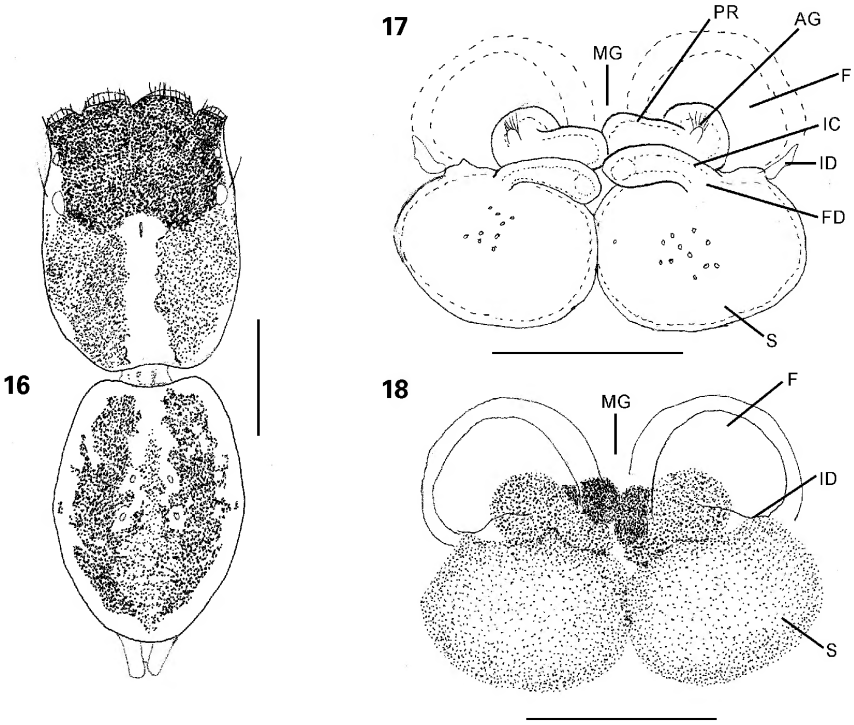
Legs I, II and IV: proximal half of femora cream dorso-anteriorly and rest dark grey with dark grey patches ventro-posteriorly; tibiae and patellae tan with dark grey bands at joints; metatarsi and tarsi cream, covered with dense short white setae interspersed with black bristles. Leg III: dorsal femur cream, rest dark grey dorsally and ventrally, patella, tibia and metatarsus tan; tibia brown; metatarsus tan, tarsus cream. Femur with dense brush of thick, short cream setae dorsally, long black/cream setae at distal joint ventrally; patella with thick brush of long black/cream setae ventrally, not as dense dorsally, small tufts of white setae above joint with metatarsus; thick brush of long black/cream setae continues onto ventral tibia and metatarsus, also dorsally but not as dense, particularly sparse on dorsal metatarsus (Figure 12); tarsus with thick, short white setae on all surfaces and longer white setae at tip, covering claws (Figure 12).

Pedipalp creamy yellow. Tibial apophysis narrow, straight (Figure 14). Cymbium, dorsal tibia and dorsal patella densely covered with long white setae, a single very long black seta on dorsal pedipalpal patella; tibia and cymbium with a few long creamy setae on ventral side just under tegulum. Embolus with broad tip and conductor closely aligned with embolus into tight coil, tucked under tip of cymbium; tegulum with two bulges adjacent to embolus (Figure 13).

Female (paratype, WAM T59143)

Ocular region black, densely covered with short creamy setae and scattered black long setae, rest of

FIGURE 15 *Maratus harveyi* sp. nov., photograph of male with folded abdominal flaps. (Image courtesy C. O'Toole).



FIGURES 16–18 *Maratus harveyi* sp. nov. female paratype (WAM T59143): 16) cephalothorax and abdomen, dorsal view; 17) cleared epigyne, dorsal view; 18) epigyne, ventral view. Scale lines = 1 mm (Figure 16), 0.25 mm (Figures 17–18). AG = accessory gland; F = fossa; FD = fertilisation duct; IC = intermediate canal; ID = insemination duct; MG = median guide; PR = proximal receiver; S = spermatheca.

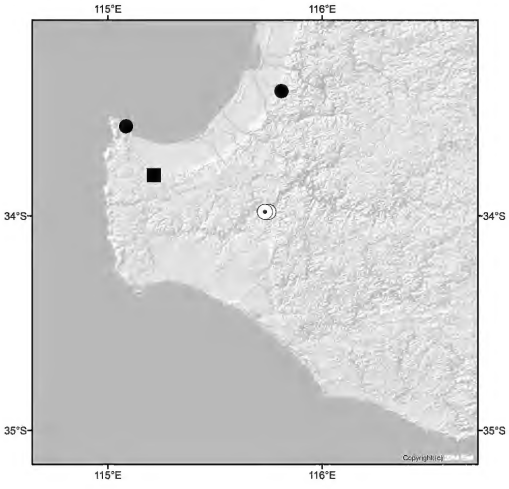


FIGURE 19 Map of collection localities of *Maratus* in south-western Western Australia: *M. fletcheri* sp. nov. (solid square); *M. harveyi* sp. nov. (open circle); *M. madelineae* (solid circle).

cephalothorax dark grey to black grading to light grey with a pale yellow band with short white setae. A broad pale yellowish strip with short white setae extends from anterior of fovea to posterior edge (Figure 16). Clypeus cream; chelicerae yellow with light grey patches, maxillae, labium cream. Sternum cream with light grey shading.

Abdomen oval with light tan dorsal sigilla and black bristles scattered amongst light brown setae; most of dorsum covered in dark grey to black patch on light cream background; patch grades to pale grey at spinnerets (Figure 16), and central patch is divided by a light grey band which extends from anterior to posterior of abdomen; edges of dorsum pale yellow with a few scattered light grey patches. Venter of abdomen light cream, with small scattered patches of grey and dark grey stripes at edges. Dorsal spinnerets cream, ventral pair cream with light grey patches.

Femora light cream with dark grey patches postero-laterally on all legs, grey patches become bands ventrally on legs III and IV; patellae creamy, no markings; tibiae of all legs creamy with greyish patches proximally and distally; rest of leg segments without banding.

Proximal receivers of epigyne tightly coiled, not extending across spermathecae to lateral edges of fossae; slightly swollen at median guide, not separated, right proximal receiver sitting ventral to left proximal receiver. Intermediate canals open at anterior margin of spermathecae from somewhat elongate tubules that extend across median guide. Insemination ducts opening at centre of posterior border of fossae. Fossae antero-posteriorly compressed ovals (Figures 17–18).

Dimensions (mm)

Holotype ♂ (paratype ♀, WAM T59143): total length (excluding chelicerae) 3.82 (4.67). Carapace length 1.84 (2.25). Abdomen length 1.66 (2.17). Leg I: femur 0.84 (0.74), patella 0.46 (0.45), tibia 0.53 (0.49), metatarsus 0.39 (0.44), tarsus 0.35 (0.39). Leg II: femur 0.79 (0.91), patella 0.41 (0.48), tibia 0.43 (0.47), metatarsus 0.37 (0.49), tarsus 0.31 (0.40). Leg III: femur 1.31 (1.61), patella 0.50 (0.69), tibia 0.69 (0.84), metatarsus 0.71 (0.85), tarsus 0.52 (0.48). Leg IV: femur 1.00 (1.30), patella 0.47 (0.36), tibia 0.60 (0.45), metatarsus 0.63 (0.96), tarsus 0.41 (0.51). Legs, relative lengths: III: IV: I: II (III: IV: II: I).

DISTRIBUTION

Maratus harveyi has only been recorded from the vicinity of Barrabup Road, Nannup, south-western Australia (Figure 19).

ETYMOLOGY

The specific epithet is in honour of Mark Harvey, senior curator of the Arachnology collection of the Western Australian Museum and co-collector of the first known specimen of this species.

Maratus madelineae Waldock, 2014

Madeline's Peacock Spider

(Figure 19)

Maratus madelineae Waldock, 2014: 150, figures 1–10.

MATERIAL EXAMINED

Australia: ***Western Australia*:** 3 ♂, Meelup Regional Park, c. 4 km NW. of Dunsborough, 33°34'56"S, 115°05'08"E, 17 September 2016, A. Fletcher, M. Doe, M. Duncan (WAM T146592–4); 2 ♀, Meelup Regional Park, c. 4 km NW. of Dunsborough, 33°34'56"S, 115°05'08"E, 17 September 2016, P. Irvine (WAM T146595–6).

DISTRIBUTION

Maratus madelineae has previously been recorded from Dardanup National Park (Waldock 2014), and the new records extend the known distribution of the species by c. 70 km SW. of the type locality.

ACKNOWLEDGEMENTS

Many thanks to Mark Harvey for providing the map. We also appreciate the helpful suggestions from Dr Michael Rix and Joseph Shubert.

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Five new species of the open-holed trapdoor spider genus *Aname* (Araneae: Mygalomorphae: Anamidae) from Western Australia, with a revised generic placement for *Aname armigera*

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ABSTRACT – The open-holed trapdoor spider genus *Aname* L. Koch, 1873 is widely distributed throughout Australia, and currently contains 44 named species. Using a combination of morphological and molecular data, we describe five new species from the Wheatbelt, Mid-west and Goldfields regions of Western Australia: *A. exulans* sp. nov., *A. lillianae* sp. nov., *A. mccleeryorum* sp. nov., *A. phillipae* sp. nov. and *A. simoneae* sp. nov. The female holotype of *Aname armigera* Rainbow and Pulleine, 1918 from near Mullewa was examined and found to belong to the genus *Proshermacha* Simon forming the new combination *P. armigera* (Rainbow and Pulleine, 1918), comb. nov.

KEYWORDS: taxonomy, systematics, molecular phylogenetics

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INTRODUCTION

The open-holed trapdoor spider genus *Aname* L. Koch, 1873 is the most diverse anamid genus with 44 named species recorded from most regions of mainland Australia. The recent detection of a diagnostic morphological feature — the ventral asetose depression on the male pedipalpal tibia — and the inclusion of numerous species of *Aname* in a comprehensive molecular phylogenetic analysis, confirm that the genus as currently recognised is monophyletic. Although, two recent publications have described 15 new species from Western Australia (Castalanelli et al. 2020; Harvey et al. 2012), there are numerous undescribed species recognised using molecular and morphological data (Castalanelli et al. 2014; Harvey et al. 2018; MSH, JAH, unpublished data).

Although a full revision of the genus is currently beyond our capacity, we here describe five new species from the Wheatbelt, Mid-west and Goldfields regions of Western Australia. Three of these species share substantial morphological similarities with *A. whitei* Castalanelli, Framenau, Huey and Harvey, 2020, a species from Western Australia recently described in a study focused on the Pilbara region (Castalanelli et al. 2020). During that study, morphologically similar specimens collected from the Goldfields and northern Wheatbelt regions of Western Australia were identified in the Western Australian Museum. Closer study of these specimens, and the acquisition of new sequence data, revealed them to represent three additional species, which can be distinguished from each other and from *A. whitei* in the divergent morphologies of the pedipalp of adult males, and sometimes also the spermathecae of females. We also describe two new species from the Mid-west region of Western Australia that possess distinct chevron patterns on the abdomen.

Finally, we also studied the female holotype of *A. armigera* Rainbow and Pulleine, 1918 from near Mullewa, as it occurs within the range of one of the new species. It was found to belong to the genus *Proshermacha* Simon, 1908. We redescribe and illustrate this species, although we have been unable to match males with the female.

MATERIALS AND METHODS

MORPHOLOGY

The specimens examined in this study are lodged in the Western Australian Museum, Perth (WAM), Queensland Museum, Brisbane (QM) and the Australian Museum, Sydney (AM), and are preserved in 75% ethanol. Auto-montaged images were taken at different focal planes (c. 20–30 images) with a Leica DFC500 digital camera attached to a Leica MZ16A stereo microscope, using Leica Application Suite (LAS) version 2.5.OR1 software.

Terminology follows Raven (1985a, 1985b) and Castalanelli et al. (2020). The following abbreviations are used: AME: anterior median eyes; ALE: anterior lateral eyes; PLE: posterior lateral eyes; PME: posterior median eyes. Pedipalp and leg measurements and ratios were calculated using the terminology and reference points defined by Castalanelli et al. (2020).

Morphological characters were scored using DELTA 1.4 (CSIRO, Canberra, Australia) (Dallwitz et al. 2010), which was also used to generate a natural language description that was subsequently edited further. The species are treated in alphabetical order.

The map was produced in ArcGIS version 10.1, with the distributions of each species superimposed over the local IBRA bioregions, as defined by Thackway and Cresswell (1995) and Environment Australia (2000). The map layers were accessed from https://www.environment.gov.au/land/nrs/science/ibra (access date 30 January 2020).

MOLECULAR METHODS

Seven genes were selected for this study, three mitochondrial DNA (mtDNA) genes (cytochrome *c* oxidase subunit I [*COI*], 12S rRNA [12S], and 16S rRNA [16S]), and four nuclear DNA (nDNA) genes (18S rRNA [18S], 28S rRNA [28S], Histone H3 [*H3*] and elongation factor 1-gamma [*EF1*]). These were the same genes used in Harvey et al. (2018) and all DNA extraction, amplification and sequencing methods follow the methods described therein. Sequences and workflows were managed with the Geneious software package (R9.0.5), using the LIMS Biocode plug-in (http://www.mooreabiocode.org).

As well as the new species described here, representative sequences were selected from 13 previously described species: *A. aragog* Harvey, Framenau, Wojcieszkek, Rix and Harvey, 2012, *A. christineae* Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020, *A. ellenae* Harvey, Framenau, Wojcieszkek, Rix and Harvey, 2012, *A. grothi* Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020, *A. kimae* Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020, *A. lorica* Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020, *A. mainae* Raven, 2000, *A. marae* Harvey, Framenau, Wojcieszkek, Rix and Harvey, 2012, *A. mellosa* Harvey, Framenau, Wojcieszkek, Rix and Harvey, 2012, *A. pallida* L. Koch, 1873, *A. sinuata* Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020, *A. watsoni* Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020 and *A. whitei* Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020 (Table 1). All of these sequences had been previously published in Harvey et al. (2018) and Castalanelli et al. (2020). The tree was rooted on *Hesperonatalius maxwelli* Castalanelli, Huey, Hillyer and Harvey, 2017, following Harvey et al. (2018), where it was demonstrated that *Hesperonatalius* was the sister lineage to *Aname*. Some of the new species described here had also been sequenced in previous publications (Castalanelli et al. 2014; Harvey et al. 2018), and GenBank was used as the source of these sequences. Each gene was aligned using the MAAFT plug-in in Geneious (Katoh et al. 2002), using the default settings. Coding genes were screened for stop codons by translating alignments, and sequences that exhibited stop codons were discarded. Ribosomal gene alignments had ambiguously aligned regions removed using G Blocks (Castresana 2000; Talavera and Castresana 2007), via the web tool (http://molevol.cmima.csic.es/castresana/Gblocks_server.html), with the settings allowing for gaps and larger blocks. Individual gene trees were built using the RaXML plug-in within Geneious Prime (Stamatakis 2006), with 1,000 bootstraps and using the Generalised time reversible with gamma correction (GTR+gamma) substitution model. The optional partitioning for the concatenated alignment was identified using Partition Finder, version 1.1 (Lanfear et al. 2012), treating each codon independently for coding genes. The optimal partitioning included three partitions; (1) 12S, 16S, *COI* positions 1 and 2, *EF1* position 3, and *H3* position 3; (2) 18S, 28S, *EF1* positions 1 and 2, *H3* positions 1 and 2; and (3) *COI* position 3. A Maximum Likelihood tree was constructed for the concatenated dataset using the RaxML plugin in Geneious Prime, with 1,000 bootstraps and GTR+gamma as the substitution model for all partitions. For the concatenated analysis, *Aname lorica*, *A. watsoni* and *A. whitei* sequences were chimeras of sequences published in Castalanelli et al. (2020), as no single specimen of these species was sequenced for every gene. Average interspecific and intraspecific p-distances were calculated for the *COI* gene using MEGA X (Kumar et al. 2018).

RESULTS AND DISCUSSION

MOLECULAR DATA

The concatenated Maximum Likelihood phylogeny included multiple specimens per species for four of the five species described in this study: *A. exulans*, *A. mcleeryorum*, *A. phillipae* and *A. simoneae*, where available, and reduced the other species to one or two specimens (Figure 1). All of these species were recovered as monophyletic, however, some with low support (*A. phillipae*, BS = 69 and *A. simoneae* BS = 72). Despite their distributions overlapping (Figure 151), the new species were not each other's closest relatives, with *A. exulans* and *A. mcleeryorum* sister to each other and most closely related to *A. mainae* from the Eyre Peninsula (South Australia). *Aname phillipae*, *A. simoneae* and

A. whitei formed a closely related clade, which was reflected in their very similar morphology. Overall, the topology presented here should be interpreted with caution as many more unsequenced and undescribed species are known, the inclusion of which could alter the relationships.

The genetic distances recovered here demonstrate the difficulty of identifying a strict species level genetic threshold in *Aname*. The *COI* p-distances revealed intraspecific genetic distances as high as 8.98% in *A. simoneae*, and interspecific distances as low as 7.5% were recovered between *A. exulans* and *A. mcleeryorum* (Table 2).

MORPHOLOGY

As noted by Raven (1985a) and Castalanelli et al. (2020), the spermathecae of female *Aname* contain significant interspecific variation. Indeed, the spermathecae of the closely related *A. exulans* and *A. mccleeryorum* described below exhibit consistent differences, despite these two species being sister-taxa and only 8% divergent on average for *COI*. In contrast, we were unable to differentiate between the females of three closely related species, *A. phillipae*, *A. simoneae* (described below) and *A. whitei*, described from the Pilbara (Castalanelli et al. 2020). As *A. phillipae* and *A. simoneae* have somewhat overlapping distributions (Figure 151), we were only able to assign females of this species group for which sequence data were available, as this represents the only guaranteed method for identifying females. The Western Australian Museum collection includes several females from the Coolgardie and Murchison IBRA bioregions that could not be identified to either species.

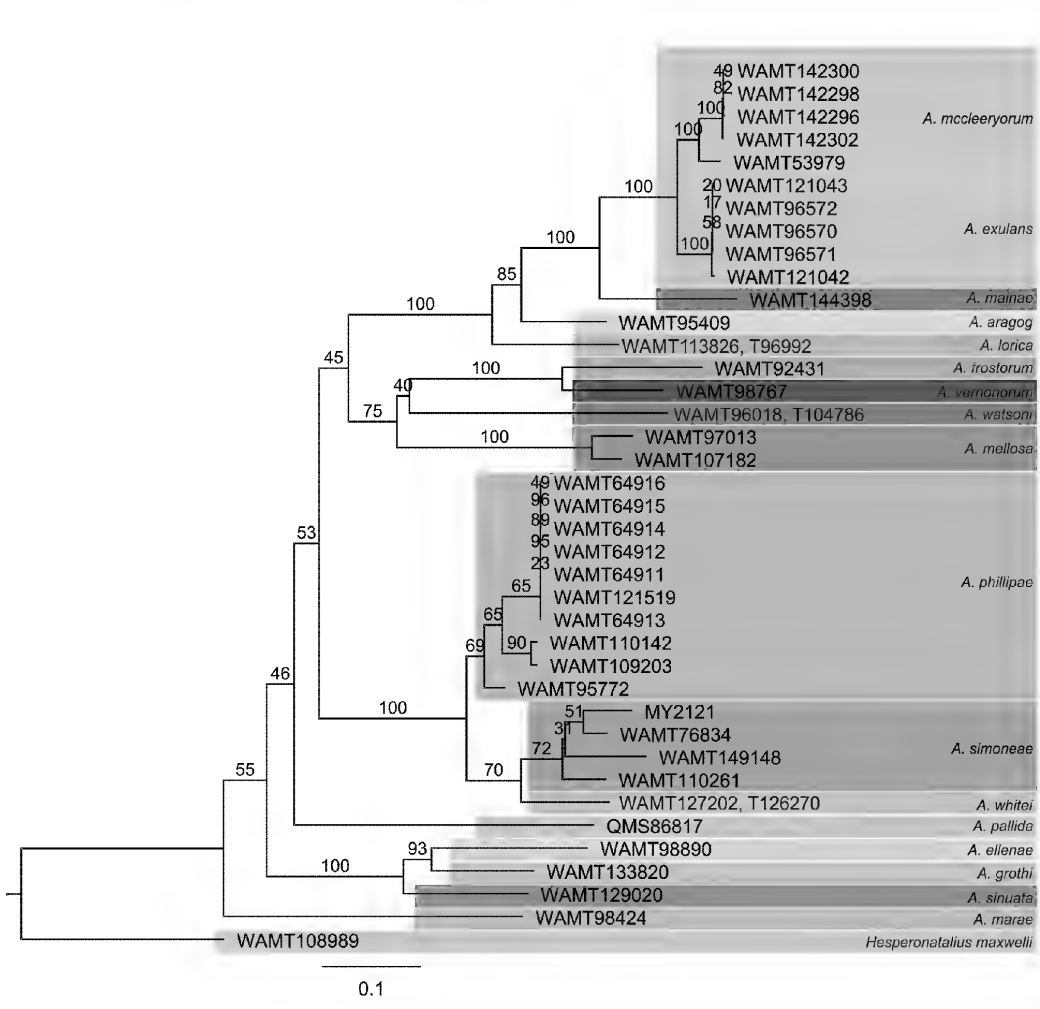


FIGURE 1 Maximum Likelihood phylogeny for the concatenated dataset. Values represent Bootstrap Values.

TABLE 1 Specimens sequenced for the molecular phylogenetic analysis (see Figure 1). Unless stated otherwise, the locations are situated in Western Australia, and specimens are lodged in the Western Australian Museum (WAM) and Queensland Museum (QM).

Taxon	Specimen	Registration number	Locality	12S	16S	18S	28S	*COI*	*EF1*	*H3*
Genus: *Aname*										
Aname exulans sp. nov.	Holotype male	WAM T96570	West Wallabi Island, Houtman Abrolhos, 28°27'24"S, 113°41'05"E	-	-	-	-	KJ745434	-	-
	Paratype male	WAM T96571	West Wallabi Island, Houtman Abrolhos, 28°27'24"S, 113°41'04"E	-	-	-	-	KJ745435	-	-
	Male	WAM T96572	East Wallabi Island, Houtman Abrolhos, 28°26'24"S, 113°44'07"E	-	-	-	-	KJ745436	-	-
	Paratype male	WAM T121042	West Wallabi Island, Houtman Abrolhos, 28°29'S, 113°41'E	MG799896	MG799962	MG800035	MG800112	MG800165	MG800236	MG800298
	Paratype male	WAM T121043	West Wallabi Island, Houtman Abrolhos, 28°29'S, 113°41'E	MT603532	MT604151	MT604134	MT604145	MT611173	MT623661	MT623670
Aname mccleeryorum sp. nov.	Holotype male	WAM T53979	Chapman Valley, 28°30'S, 114°47'E	MT603527	MT604146	MT604125	MT604135	MT611168	-	MT623663
	Juvenile	WAM T142296	Lesueur National Park, c. 380 m N. of University Track, 30°09'02"S, 115°14'09"E	MT603528	MT604147	MT604130	MT604139	MT611169	-	MT623671
	Paratype female	WAM T142298	Lesueur National Park, University Track, western end, 30°09'33"S, 115°12'14"E	MT603529	MT604148	MT604131	MT604136	MT611170	-	MT623672
	Juvenile	WAM T142300	Lesueur National Park, 30°10'54"S, 115°15'01"E	MT603529	MT604148	MT604132	MT604137	MT611171	-	MT623672

Taxon	Specimen	Registration number	Locality	12S	16S	18S	28S	*COI*	*EF1*	*H3*
	Paratype female	WAM T142302	Coorow-Green Head Road, 30°03'47"S, 115°10'44"E	MT603531	MT604150	MT604133	MT604138	MT611172	-	MT623674
Aname phillipae sp. nov.	Holotype male	WAM T110142	Deception Hill, 111.15 km NNW. of Koolyanobbing, 29°51'56"S, 119°16'37"E	-	MT604160	MT604128	MT604141	-	MT623659	MT623668
	Paratype male	WAM T95772	S. of Kambalda, 31°34'03"S, 121°44'42"E	-	-	-	MT604143	-	-	MT623667
	Paratype male	WAM T109203	Deception Hill, 93.10 km NNW. of Koolyanobbing, 30°02'06"S, 119°16'28"E	-	MT611177	-	-	MT604159	-	-
	Male	WAM T64911	Lord Nelson [mine], 10.3 km SSW. of Black Hill, site LN03, 28°09'36"S, 119°30'36"E	-	MT604152	MT604126	MT604140	-	MT623657	MT623664
	Male	WAM T64912	Lord Nelson [mine], 10.3 km SSW. of Black Hill, site LN03, 28°09'36"S, 119°30'36"E	-	MT604153	-	-	-	-	MT623665
	Male	WAM T64913	Lord Nelson [mine], 10.3 km SSW. of Black Hill, site LN03, 28°09'36"S, 119°30'36"E	-	-	-	-	-	MT623658	-
	Male	WAM T64914	Lord Nelson [mine], 10.3 km SSW. of Black Hill, site LN03, 28°09'36"S, 119°30'36"E	-	MT604154	-	-	-	-	-
	Male	WAM T64915	Lord Nelson [mine], 10.3 km SSW. of Black Hill, site LN03, 28°09'36"S, 119°30'36"E	-	MT604155	-	-	-	-	-
	Male	WAM T64916	Lord Nelson [mine], 10.3 km SSW. of Black Hill, site LN03, 28°09'36"S, 119°30'36"E	-	MT604156	-	-	-	-	-
	Male	WAM T121519	Mt Ida, 80 km NW. of Menzies, 29°11'01"S, 120°25'18"E	-	-	-	-	-	MT623662	-

Taxon	Specimen	Registration number	Locality	12S	16S	18S	28S	*COI*	*EF1*	*H3*
Aname simoneae sp. nov.	Holotype male	WAM T110261	21 km S. of Laverton, 28°47'34"S, 122°25'53"E	-	MT604158	MT604129	MT604144	MT611175	MT623660	MT623669
	Paratype female	WAM T149148	c. 41.5 km SSE. of Menzies. 30°04'21.91"S, 121°10'35.75"E	-	-	-	-	MT611176	-	-
	Juvenile	WAM T76834	Wanjarri, 53.3 km S. of Lake Way homestead, site YAK07B, 27°24'24"S, 120°36'42"E	-	MT604157	MT604127	MT604142	MT611174	-	MT623666
	Unknown	MY2121	N. of Leonora S28.10172 E121.90417 (Hedin and Bond 2006)	KY015478	KY015978	DQ639832	KY017209	KY017804	-	KY018318
Aname aragog Harvey, Framenau, Wojcieszek, Rix and Harvey, 2012	Female	WAM T95409	Jimblebar minesite, 35 km E. of Newman, 23°22'44"S, 120°15'27"E	KY214181	KY241234	KY241250	KY241265	KJ745403	MG800219	KY241287
Aname ellenae Harvey, Framenau, Wojcieszek, Rix and Harvey, 2012	Holotype male	WAM T98890	Aquila Onslow, 24.9 km SE. of Onslow, 21°46'56"S, 115°17'40"E	KY214186	KY241238	KY241255	KY241270	JQ772138	-	KY241291
Aname frostorum Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020	Paratype male	WAM T92431	11 km SSE. of Whim Creek Hotel, 20°55'11.4"S, 117°51'40.6"E	MN634950	-	-	-	-	-	-
Aname grothi Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020	Holotype male	WAM T133820	Great Sandy Desert, 90 km SW. of Wangkatjungka, 19°32'30"S, 125°24'06"E	MN634958	MN634775	MN634925	MN634748	MN635075	-	MN635127
Aname lorica Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020	Paratype male	WAM T113826	Barrow Island, 20°41'32"S, 115°25'4"E	MN634945	MN634841	MN634935	MN634733	-	MN635140	MN635093
	Male	WAM T96992	Barrow Island, 20°49'35"S, 115°26'44"E	-	-	-	-	MN635038	-	-
Aname mainae Raven, 2000	Female	WAM T144398	South Australia: Corner of Flinders Highway and Talia Caves Road, 33°17'25"S, 134°49'23"E	MN634938	MN634859	-	MN634735	MN635077	-	MN635092

Taxon	Specimen	Registration number	Locality	12S	16S	18S	28S	*COI*	*EF1*	*H3*
Aname marae Harvey, Framenau, Wojcieszek, Rix and Harvey, 2012	Holotype male	WAM T98424	Tom Price powerlines, 4 km NW. of Tom Price, 22°41'10"S, 117°44'56"E	KY214185	-	KY241254	KY241269	JQ772144	-	KY241290
Aname mellosa Harvey, Framenau, Wojcieszek, Rix and Harvey, 2012	Paratype male	WAM T97013	Jinayri, c. 65 km NW. of Newman, 22°51'10"S, 119°16'34"E	KY214184	KY241237	KY241253	KY241268	JQ772134	-	-
	Male	WAM T107182	Fortescue Marsh, 22°18'26.28"S, 119°12'57.24"E	MG799892	MG799958	MG800030	MG800107	KJ744651	MG800231	MG800294
Aname pallida L. Koch, 1873	Female	QM S86817	Queensland: Prosperine, Thompson Creek, 20°30'S, 148°34'E	KY214179	KY241230	-	-	KY241278	-	KY241283
Aname sinuata Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020	Paratype male	WAM T129020	Cape Lambert, 3 km N. of Wickham, 20°38'56"S, 117°08'47"E	MN634957	MN634758	MN634924	MN634745	MN635073	MN635131	MN635099
Aname vernonorum Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020	Paratype male	WAM T98767	Aquila Onslow, 24.9 km SE. of Onslow, 21°46'56"S, 115°17'40"E	MG799887	MG799953	MG800025	MG800102	MG800161	MG800226	MG800290
Aname watsoni Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020	Paratype female	WAM T96018	Jimblebar, c. 35 km E. of Newman, 23°22'52"S, 120°10'24"E	MN634960	MN634776	MN634929	MN634750	-	-	MN635125
	Holotype male	WAM T104786	8 km W. of Newman, 23°23'01.35"S, 119°38'52.06"E	-	-	-	-	MN635068	-	-
Aname whitei Castalanelli, Framenau, Huey, Hillyer and Harvey, 2020	Juvenile	WAM T127202	78.2 km NW. of Newman, 23°01'11"S, 119°03'36"E	-	MN634900	MN634928	MN634726	-	MN635134	MN635108
	Female	WAM T126270	114 km NW. of Newman, 22°36'52"S, 118°57'18"E	-	-	-	-	MN635083	-	-
Genus: *Hesperonatalius*										
Hesperonatalius maxwelli Castalanelli, Huey, Hillyer and Harvey, 2017	Paratype male	WAM T108989	Lake MacLeod, 24°28'33.9"S, 113°31'32.7"E	KY214190	KY241244	KY241259	KY241275	KJ744690	MG800233	KY241293

TABLE 2 Average *COI* between-species p-distance. Average within-species p-distance in bold (only shown for species newly described in this manuscript). The number of *COI* sequences available for each of the new species is given in parentheses.

	A. simoneae	*A. whitei*	*A. phillipae*	*A. mccleeryorum*	*A. exulans*	*A. mainae*	*A. aragog*	*A. pallida*	*A. ellenae*	*A. sinuata*	*A. grothi*	*A. vernonorum*	*A. mellosa*	*A. lorica*	*A. watsoni*	*A. marae*
A. simoneae (n=4)	**0.09**															
A. whitei	0.13															
A. phillipae (n=1)	0.15	0.14	**0.00**													
A. mccleeryorum (n=5)	0.18	0.18	0.16	**0.03**												
A. exulans (n=5)	0.18	0.18	0.15	0.08	**0.00**											
A. mainae	0.17	0.17	0.17	0.14	0.14											
A. aragog	0.18	0.17	0.15	0.17	0.16	0.15										
A. pallida	0.18	0.18	0.17	0.17	0.17	0.16	0.15									
A. ellenae	0.18	0.17	0.15	0.16	0.16	0.15	0.16	0.17								
A. sinuata	0.17	0.16	0.16	0.18	0.17	0.15	0.17	0.15	0.13							
A. grothi	0.17	0.17	0.14	0.17	0.16	0.16	0.16	0.14	0.13	0.13						
A. vernonorum	0.16	0.16	0.16	0.15	0.16	0.16	0.17	0.14	0.15	0.17	0.15					
A. mellosa	0.18	0.19	0.16	0.19	0.18	0.16	0.16	0.15	0.16	0.16	0.16	0.17				
A. lorica	0.17	0.18	0.17	0.17	0.19	0.19	0.17	0.19	0.17	0.18	0.17	0.17	0.18			
A. watsoni	0.18	0.18	0.16	0.18	0.18	0.16	0.17	0.17	0.15	0.18	0.15	0.15	0.16	0.15		
A. marae	0.18	0.18	0.16	0.17	0.17	0.16	0.18	0.17	0.16	0.15	0.16	0.17	0.19	0.17	0.17	

SYSTEMATICS

Family Anamidae Simon, 1889

Genus *Aname* L. Koch, 1873

Aname L. Koch, 1873: 465. Type species: *Aname pallida* L. Koch, 1873, by monotypy.

Dekana Hogg, 1902: 138 (synonymised by Raven, 1981: 328). Type species: *Dekana diversicolor* Hogg, 1902, by original designation.

Sungenia Rainbow and Pulleine, 1918: 162 (synonymised by Raven, 1981: 328). Type species: *Chenistonia (Dekana) atra* Strand, 1913, by monotypy.

Dolichosternum Rainbow and Pulleine, 1918: 168 (synonymised by Raven, 1981: 328). Type species: *Dolichosternum attenuatum* Rainbow and Pulleine, 1918 (junior synonym of *Ixamatus distinctus* Rainbow, 1914), by monotypy.

DIAGNOSIS

Species of *Aname* can be distinguished from all other anamids by the presence of prominent asetose ventral depression on the male pedipalpal tibia (Figures 15, 44, 73, 104, 133).

Aname exulans Harvey and Huey, sp. nov.

Figures 2–30

urn:lsid:zoobank.org:act:E1C159C4-DA92-44D2-8393-92927BBC4512

Aname 'MYG067': Castalanelli 2014: fig. 3.

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** ♂, West Wallabi Island, Houtman Abrolhos, 28°27'24"S, 113°41'05"E, 10 January 2008, dry pitfall trap, R. Teale, Z. Hamilton, R.A. How (WAM T96570 DNA).

Paratypes

Australia: ***Western Australia:*** 3 ♀, North Island, Houtman Abrolhos, 28°18'S, 113°36'E, 27 August 1974, Aquinas Boys College (WAM T10124–10126); 1 ♀, North Island, Houtman Abrolhos, 28°18'S, 113°36'E, 3 August 1976, R. Prince (WAM T47464); 2 ♂, West Wallabi Island, Houtman Abrolhos, 28°27'24"S, 113°41'04"E, 11 January 2008, dry pitfall trap, M.A. Cowan, D. Kamien (WAM T96571 DNA, T96576); 1 ♂, West Wallabi Island, Houtman Abrolhos, 28°28'04"S, 113°41'13"E, 11 February 2012, dry pitfall trap, C.A. Stevenson, M.A. Cowan, P. Spencer, P. Kendrick (WAM T120851); 1 ♂, West Wallabi Island, Houtman Abrolhos, 28°29'S, 113°41'E, 10 February 2012, C. Stevenson (WAM T121042 DNA); 2 ♂, same data except 7 February 2012 (WAM T121043 DNA, T121044).

Other material

Australia: ***Western Australia:*** 1 ♂, 1 juvenile, East Wallabi Island, Houtman Abrolhos, 28°26'24"S, 113°44'07"E, 10 January 2008, dry pitfall trap, R. Teale, Z. Hamilton, R.A. How (WAM T96572 DNA, T96575); 4 ♂, 1 juvenile, West Wallabi Island, Houtman Abrolhos, 28°27'24"S, 113°41'05"E, 8–11 November 2005, dry pitfall trap, R.A. How, et al. (WAM T77027); 1 juvenile, Houtman Abrolhos, East Wallabi Island, 28°26'S, 113°43'E, 9 December 1968, A.R. Main (WAM T147673).

DIAGNOSIS

Aname exulans is easily distinguished from all other named species of *Aname* by the abdominal colour pattern which comprises a pale background, a dark median stripe and several indistinct chevrons (Figures 9, 27).

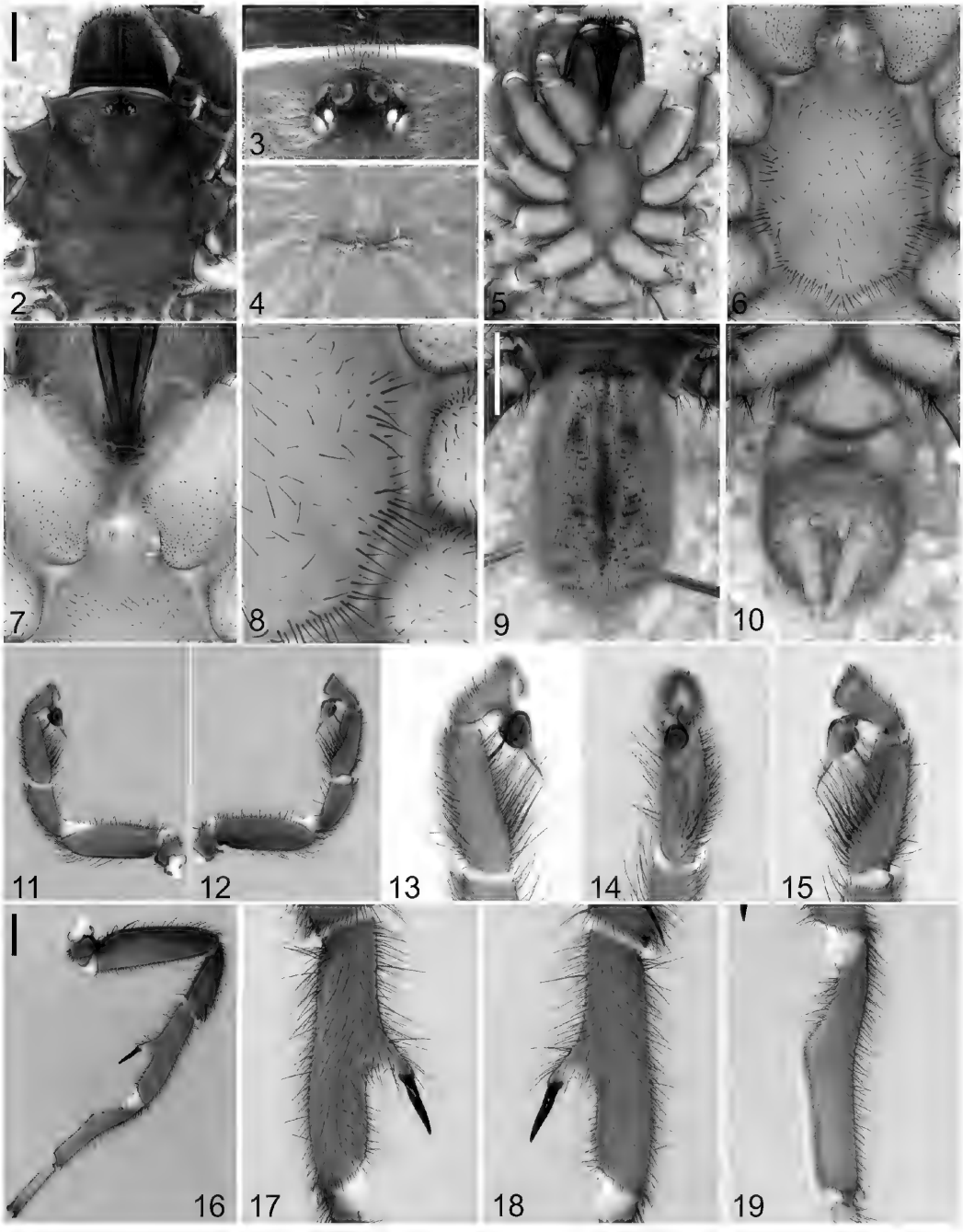
Aname exulans most closely resembles *A. mccleeryorum* as the females of both species have distinct chevron patterning on the abdomen. However, the abdomen has a dark median stripe and several indistinct chevrons in *A. exulans* (Figure 27) but is diffusely grey on a light background in *A. mccleeryorum* (Figures 85, 90). Males of *A. exulans* differ from *A. mccleeryorum* in the shape of the pedipalp including the longer tibial depression and the longer and straighter embolus (Figures 13–15). Females differ by the coiled and distally bifurcate spermathecal lobes (Figures 29, 30), which are short and slightly curved in *A. mccleeryorum* (Figures 87, 88).

DESCRIPTION

Male: based on holotype (WAM T96570)

Colour (in alcohol): Carapace anterior brown-yellow fading to yellow-brown posteriorly; legs brown, some segments with longitudinal pale stripes, tarsi paler; chelicerae uniformly dark red-brown; abdomen dorsally pale yellow-brown with black median stripe and several indistinct chevrons, and ventrally pale yellow-brown.

Cephalothorax: Carapace (Figure 2) 1.26 × longer than broad; with sparse fine setae, silver hairs present, with brown bristles dorsally. Clypeal edge protruding medially. Fovea slightly procurved (Figure 4). Eyes on distinct mound (Figure 3); from above, anterior eye row slightly procurved, posterior eye row slightly recurved; AME about same size as ALE; ALE and AME the largest; PME smallest; eye group length 0.7, width 1.2. Chelicerae with broad dorsal strip of black setae, and two thinner lateral strips of smaller black setae; rastellum absent; promargin of tooth row with 9 teeth, retromargin with 6 teeth. Labium fused to sternum (Figure 7); without cuspules. Maxillae (Figure 7) with 220 cuspules, located on basal third. Sternum (Figure 6): oval, posteriorly pointed; 1.18 × longer than broad;



FIGURES 2–19 *Aname exulans* sp. nov., holotype male (WAM T96570): 2) cephalothorax, dorsal view; 3) ocular region; 4) fovea; 5) cephalothorax, ventral view; 6) sternum, ventral view; 7) maxillae and labium, ventral view; 8) left sigilla, ventral view; 9) abdomen, dorsal view; 10) abdomen, ventral view; 11) left pedipalp, prolateral view; 12) left pedipalp, retrolateral view; 13) left pedipalp, tibia and tarsus, prolateral view; 14) left pedipalp, tibia and tarsus, ventral view; 15) left pedipalp, tibia and tarsus, retrolateral view; 16) left leg I, prolateral view; 17) left leg I, tibia I, retrolateral view; 18) left leg I, tibia I, prolateral view; 19) left leg I, metatarsus I, prolateral view. Scale lines = 2 mm.

bristles sparsely distributed over entire surface; with 3 pairs of sigilla (Figure 8), each pair increasing in size from anterior to posterior; anterior and median pairs located near edge of sternum; posterior pair elongate.

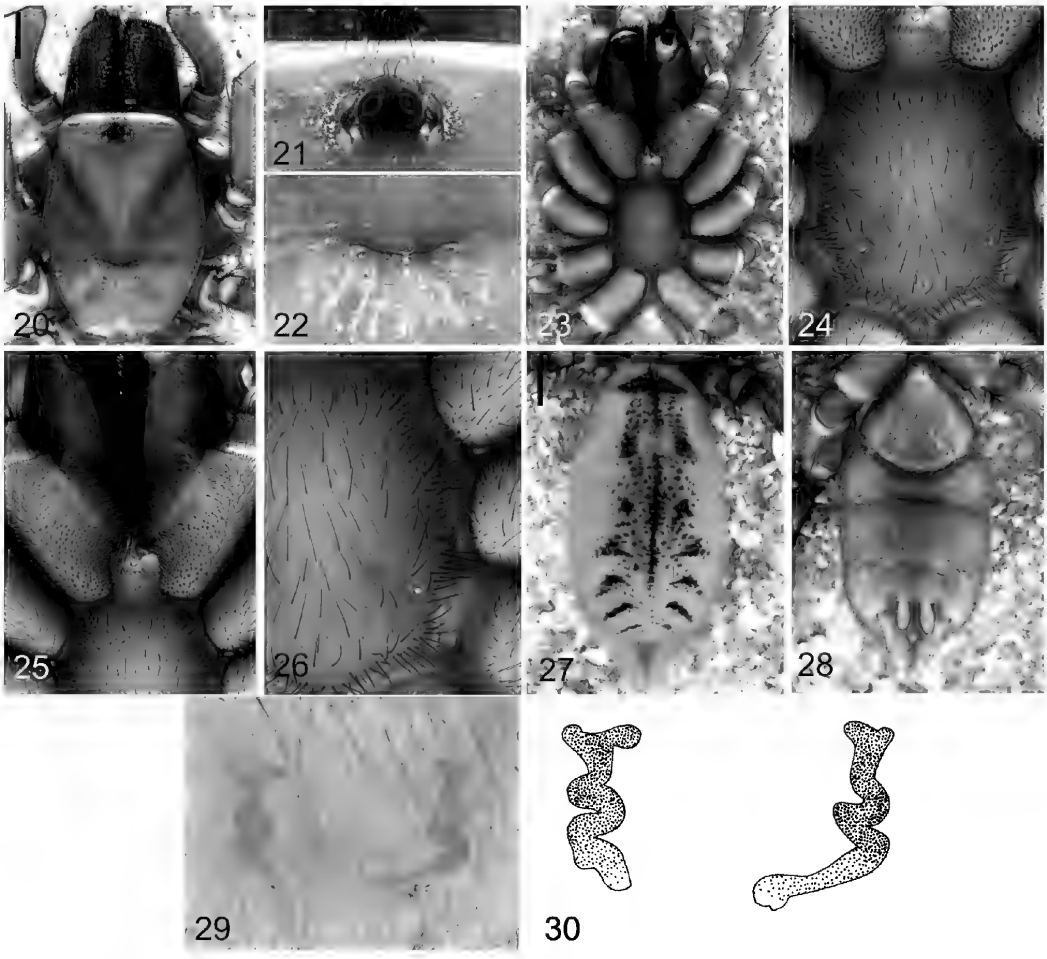
Pedipalp (Figures 11–15): Tibia cylindrical, narrow; asetose depression present, about the length of embolus; PDL/PTL 0.67. Tarsus short; sparsely setose; bulb ovoid; embolus much longer than bulb, gently curved.

Legs: Coxal cuspules absent (Figure 5). Tibia I with large megaspur (Figures 16–18); TIL/TID 4.38; TIS/TIL 0.52; TISH/TID 0.84; metatarsus incrassate (Figure 19); MIL/MID 5.00; MIPEL/MIL 0.41. Scopula present on all tarsi, metatarsi I and II, and distal half of metatarsi III and IV. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 6.2, tibia 6.6, metatarsus 5.5. Leg II: femur 5.6. Leg III: femur 4.6. Leg IV: femur 6.2.

Abdomen (Figures 9, 10): 1.8 × longer than broad, sparsely pilose with long setae on dorsal side. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Dimensions (mm): Total body length 20.0; carapace length 8.3, width 6.6; sternum length 3.9, width 3.3; abdomen length 7.5, width 4.2.

Variation: N = 10. Carapace length 7.7–8.7; width 6.4–7.1; femur I length 6.3–7.0; metatarsus I length 5.0–5.6; femur IV length 6.1–6.8.



FIGURES 20–30 *Aname exulans* sp. nov., paratype female (WAM T10124): 20) cephalothorax, dorsal view; 21) ocular region; 22) fovea; 23) cephalothorax, ventral view; 24) sternum, ventral view; 25) maxillae and labium, ventral view; 26) left sigilla, ventral view; 27) abdomen, dorsal view; 28) abdomen, ventral view; 29) spermathecae, dorsal view; 30) spermathecae, dorsal view, line drawing. Scale lines = 2 mm.

Female: based on paratype (WAM T10124).

Colour (in alcohol): Carapace anterior red-brown fading posteriorly to light brown; legs brown, some segments with longitudinal pale stripes, tarsi paler; chelicerae uniformly dark red-brown; abdomen dorsally pale yellow-brown with black median stripe and several distinct chevrons, and ventrally pale yellow-brown.

Cephalothorax: Carapace (Figure 20) 1.18 × longer than broad; with sparse fine setae, silver hairs absent, with brown bristles dorsally. Clypeal edge protruding medially. Fovea slightly procurved (Figure 22). Eyes on distinct mound (Figure 21); from above, anterior eye row slightly procurved, posterior eye row slightly recurved; AME about same size as ALE; ALE and AME the largest; PME smallest; eye group length 0.7, width 1.3. Chelicerae with broad dorsal strip of black setae, and two thinner lateral strips of smaller black setae; rastellum absent; promargin of tooth row with 9 teeth, retromargin with 5 teeth. Labium fused to sternum (Figure 25); without cuspules. Maxillae (Figure 25) with 225 cuspules; located on basal half. Sternum (Figure 24): oval, posteriorly pointed; 1.18 × longer than broad; bristles sparsely distributed over entire surface; with 3 pairs of sigilla (Figure 26), each pair increasing in size from anterior to posterior; anterior and median pairs located near edge of sternum; posterior pair elongate.

Pedipalp: Tarsus densely setose.

Legs: Coxal cuspules absent (Figure 23). Scopula present on all tarsi, present on metatarsi I and II, present on distal half of metatarsi III and IV. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg II: femur 6.0. Leg III: femur 5.5. Leg IV: femur 6.6.

Abdomen (Figures 27, 28): 1.7 × longer than broad, sparsely pilose with long setae on dorsal side. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Genitalia (Figures 29, 30): 1 pair of spermathecae, each coiled and distally bifurcate.

Dimensions (mm): Total body length 25.8; carapace length 8.7, width 7.4; sternum length 4.5, width 3.8; abdomen length 11.1, width 6.4.

Variation: N = 3. Carapace length 10.4–10.6; width 8.5–8.9; femur I length 7.5–7.6; femur IV length 7.3–8.1.

DISTRIBUTION

Aname exulans has only been found on three islands of the Houtman Abrolhos Group (North Island, West Wallabi Island and East Wallabi Island), which are located c. 60 km from the Western Australian coast in the Geraldton Sandplains IBRA bioregion of Western Australia (Figure 151).

REMARKS

Despite examining many collections of *Aname* specimens from mainland Australia, we have not detected specimens of *A. exulans* from anywhere other than the Houtman Abrolhos (Figure 151) where it is likely to be endemic. The occurrence of a species of *Aname* that is apparently endemic to the Abrolhos Islands is somewhat remarkable, given that the islands have been connected to mainland Australia as recently as 6,500 years ago (Collins et al. 2006).

SEQUENCE DATA

Intraspecific genetic divergence for this species was low, reaching only 0.06% at *COI*. It was also very closely related to its morphologically distinct sister species, *A. mcleeryorum* (7.5%), found on the mainland adjacent to the islands inhabited by *A. exulans* (Figure 151). Sequence data for a specimen of this species was supplied by Castalanelli et al. (2014) using the code *Aname* 'MYG067'.

ETYMOLOGY

The species epithet refers to the presence of this species on offshore islands (*exul*, Latin, a banished person, exile) (Brown 1956).

Aname lillianae Harvey and Huey, sp. nov.

Figures 31–59

urn:lsid:zoobank.org:act:F5610B98-5EB0-4E0A-931C-CC26A2F2E1EA

MATERIAL EXAMINED

Holotype

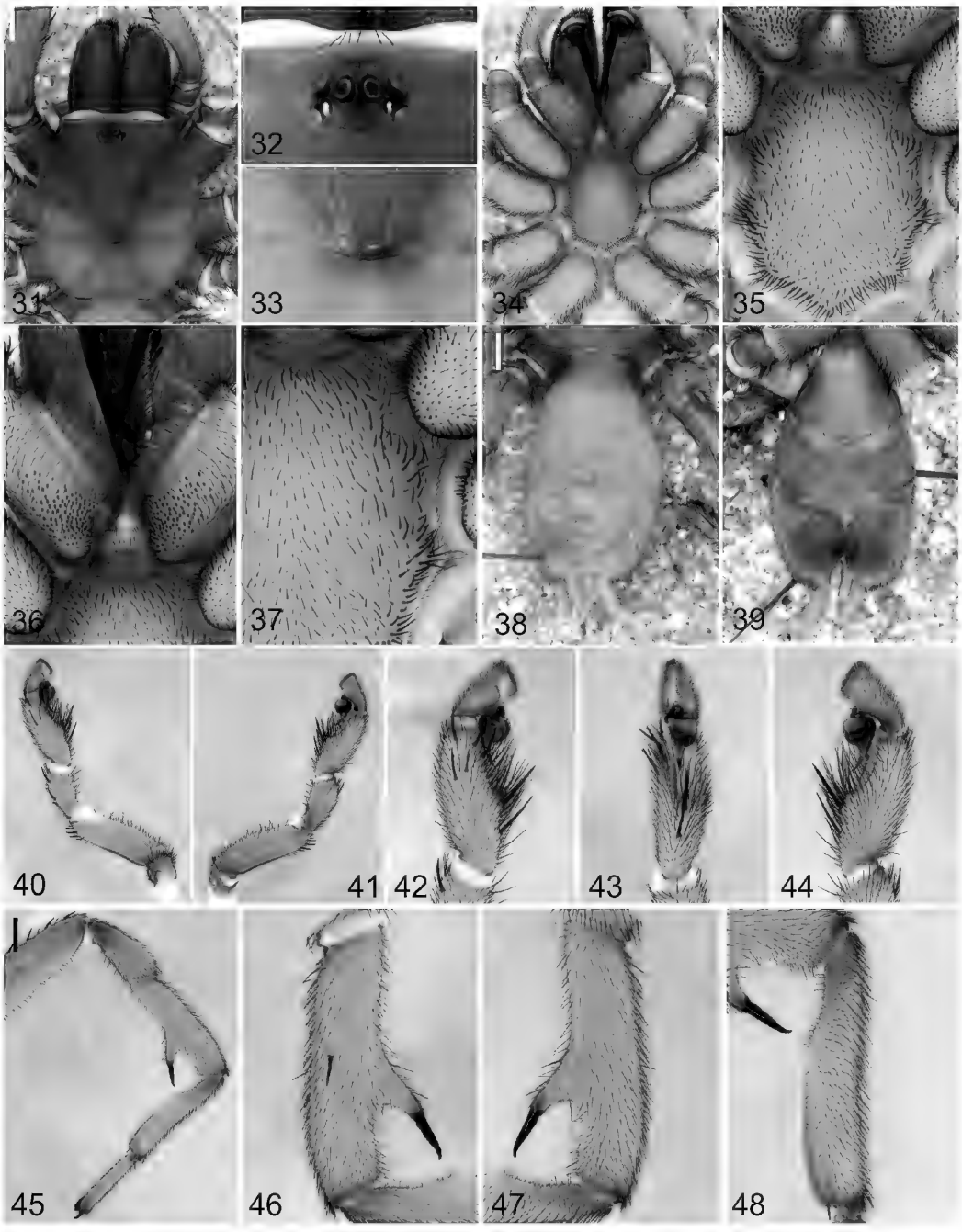
Australia: ***Western Australia:*** ♂, Pallottine Mission, near Tardun, 28°47'S, 115°51'E, collection date unknown, donated February 1990, W.H. van Veen (WAM T20639, formerly 90/609).

Paratypes

Australia: ***Western Australia:*** 1 ♂, Tutanning Nature Reserve, c. 32°32'S, 117°19'E, 29 January 1987, G.T. Smith et al. (WAM T146038); 1 ♀, Tutanning Nature Reserve, c. 32°32'S, 117°19'E, 20 October 1987, G.T. Smith et al. (WAM T146039).

Other material

Australia: ***Western Australia:*** 2 ♂, Blue Hill Range, 29°08'38"S, 116°53'40"E, 13–16 February 2004, dry pitfall, ironstone ridge in mulga/eucalypt woodland, M. Bamford (WAM T46816); 1 ♂, Cogla Downs Station, 70 miles NNW. of Sandstone, 27°26'S, 118°56'E, January 1982, A.R. Humphries (WAM T18133, formerly 88/110); 1 ♂, Coolgardie, 30°57'S, 121°10'E, 26 February 1993, donated via Department of Conservation and Land Management, Kalgoorlie (WAM T27271, formerly 93/587); 1 ♂, Durokoppin Nature Reserve, 31°24'37"S, 117°45'37"E, 6 August 1987, pitfall trap, G.R. Friend (WAM T142375); 1 ♂, Marloo Station, c. 20 miles W. of Yalgoo, 28°19'S, 116°11'E, 31 January 1968, A.M. Douglas, L.E. Koch (WAM T29852, formerly 94/263);



FIGURES 31–48 *Aname lillianae* sp. nov., holotype male (WAM T20639): 31) cephalothorax, dorsal view; 32) ocular region; 33) fovea; 34) cephalothorax, ventral view; 35) sternum, ventral view; 36) maxillae and labium, ventral view; 37) left sigilla, ventral view; 38) abdomen, dorsal view; 39) abdomen, ventral view; 40) left pedipalp, prolateral view; 41) left pedipalp, retrolateral view; 42) left pedipalp, tibia and tarsus, prolateral view; 43) left pedipalp, tibia and tarsus, ventral view; 44) left pedipalp, tibia and tarsus, retrolateral view; 45) left leg I, prolateral view; 46) left leg I, tibia I, retrolateral view; 47) left leg I, tibia I, prolateral view; 48) left leg I, metatarsus I, prolateral view. Scale lines = 2 mm.

1 ♂, McClellands [= McLennans], c. 10 km NW. of Kellerberrin, 31°34'40"S, 117°37'58"E, 10 March 1987, G.T. Smith et al. (WAM T146035); 1 ♂, Merredin, 31°29'S, 118°16'E, 15 January 1930, collector unknown (WAM T2213, formerly 30/51); 1 ♂, Ryans, c. 29 km NE. of Kellerberrin, 31°23'S, 117°51'E, 27 January 1987, G.T. Smith et al. (WAM T146036).

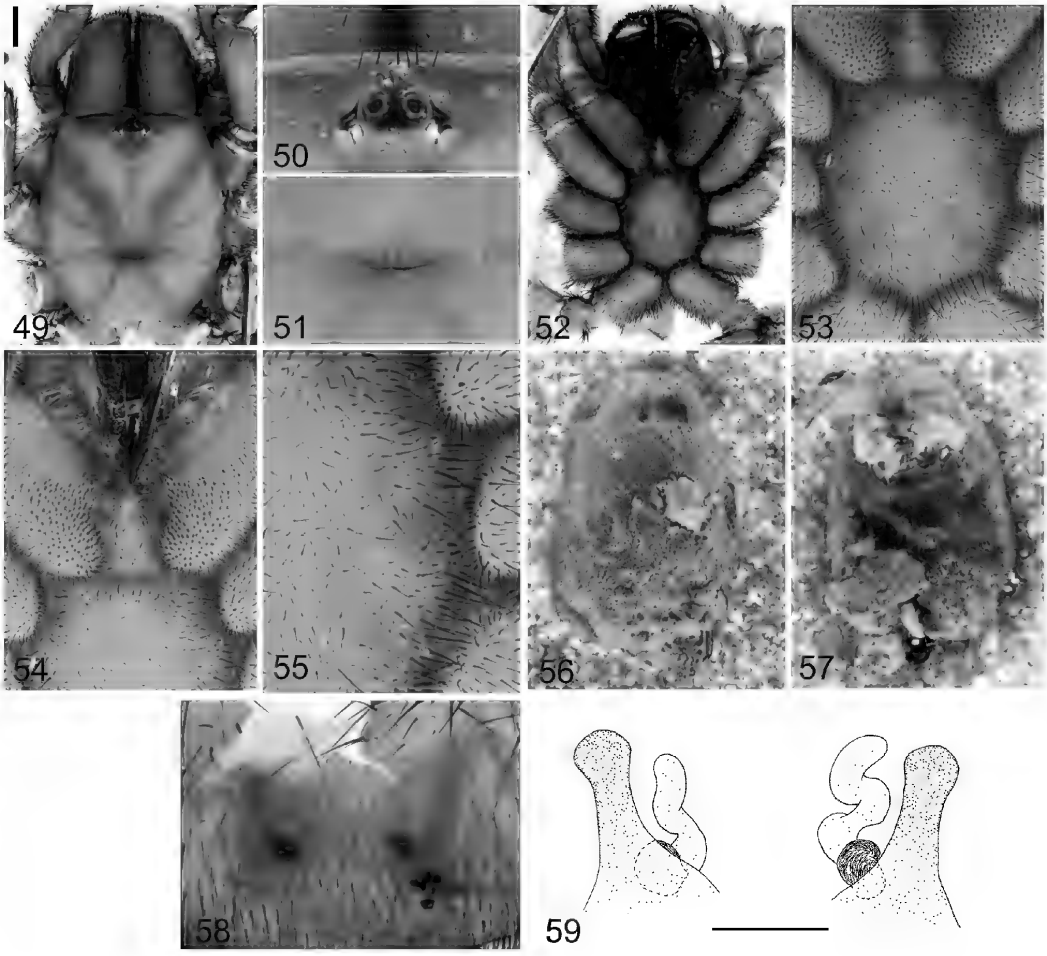
DIAGNOSIS

Aname lillianae most closely resembles *A. whitei*, *A. simoneae* and *A. phillipae* as adults of all three species are large and rather pale, with extremely thin third sigilla (Figures 37, 55). Males differ from *A. whitei*, *A. simoneae* and *A. phillipae* by the tapering, slender embolus (Figure 44), whereas the embolus of *A. whitei* and *A. simoneae* is thickened and flattened, and the embolus of *A. phillipae* has a small distinct hook. The female genitalia (Figures 58, 59) differ from all other species of *Aname* in the possession of 2 pairs of spermathecae, with the median pair slightly coiled, and the lateral pair straight and with a slightly bulbous head.

DESCRIPTION

Male: based on holotype (WAM T20639)

Colour (in alcohol): Carapace anterior red-brown fading posteriorly to light brown; legs yellow-brown with red-brown distal and basal portions; chelicerae deep red-brown; abdomen dorsally pale creamy-yellow, and ventrally pale creamy-yellow.



FIGURES 49–59 *Aname lillianae* sp. nov., paratype female (WAM T146039): 49) cephalothorax, dorsal view; 50) ocular region; 51) fovea; 52) cephalothorax, ventral view; 53) sternum, ventral view; 54) maxillae and labium, ventral view; 55) left sigilla, ventral view; 56) abdomen, dorsal view (damaged); 57) abdomen, ventral view (damaged); 58) spermathecae, dorsal view; 59) spermathecae, dorsal view, line drawing. Scale lines = 2 mm.

Cephalothorax: Carapace (Figure 31) 1.09 × longer than broad; with sparse fine setae, silver hairs present, with brown bristles dorsally. Clypeal edge protruding medially. Fovea slightly procurved (Figure 33). Eyes on distinct mound (Figure 32); from above, anterior eye row slightly procurved, posterior eye row slightly recurved; PME same size as AME; ALE and AME the largest; PME smallest; eye group length 1.03, width 1.92. Chelicerae with broad dorsal strip of black setae, and two thinner lateral strips of smaller black setae; rastellum absent; promargin of tooth row with 12 teeth, retromargin with 2 teeth. Labium fused to sternum (Figure 36); without cuspules. Maxillae (Figure 36) with 117 cuspules; located on basal third. Sternum (Figure 35): oval, posteriorly pointed; 1.12 × longer than broad; bristles over entire surface; with 3 pairs of sigilla (Figure 37), each pair increasing in size from anterior to posterior; posterior pair elongate and slightly curved; anterior pair located near edge of sternum.

Pedipalp (Figures 40–44): Tibia cylindrical, narrow; asetose depression present, about the length of embolus; PDL/PTL 0.50; densely setose; bulb globular; embolus about same length as bulb, gently curved.

Legs: Coxal cuspules absent (Figure 34). Tibia I with large megaspur (Figures 45–47); TIL/TID 4.23; TIS/TIL 0.66; TISH/TID 0.80; metatarsus slightly incrassate (Figure 48); MIL/MID 5.12; MIPEL/MIL 0.40. Scopula present on all tarsi, and metatarsi I and II. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 9.5, tibia 8.0, metatarsus 7.3. Leg II: femur 9.3. Leg III: femur 8.5. Leg IV: femur 10.4.

Abdomen (Figures 38, 39): 1.5 × longer than broad, sparsely pilose with long setae on dorsal side. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Dimensions (mm): Total body length 24.5; carapace length 10.9, width 10.0; sternum length 5.7, width 5.0; abdomen length 11.6, width 8.0.

Variation: N = 10; carapace length 9.8–12.5; width 8.9–10.8; femur I length 8.4–10.2; metatarsus I length 6.5–7.7; femur IV length 8.9–10.9.

Female: based on paratype (WAM T146039).

Colour (in alcohol): Carapace uniformly red-brown; legs uniformly red-brown; chelicerae uniformly dark red-brown; abdomen dorsally pale creamy-yellow, and ventrally pale creamy-yellow.

Cephalothorax: Carapace (Figure 49) 1.19 × longer than broad; with sparse fine setae, silver hairs absent, with brown bristles dorsally. Clypeal edge protruding medially. Fovea slightly procurved (Figure 51). Eyes (Figure 50) on distinct mound; from above, anterior eye row nearly straight, posterior eye row slightly recurved; AME about same size as PME; ALE and AME the largest; PME smallest; eye group length 1.0, width 1.88. Chelicerae with short black setae, sparsely distributed, 1 well-defined prolateral strip dense, long, and brown or black setae; rastellum absent; promargin of tooth row with 10, retromargin with 4. Labium fused to sternum (Figure 54); without cuspules. Maxillae (Figure 54) with c. 125 cuspules; located on basal third. Sternum (Figure 53): oval, posteriorly pointed; 1.1 × longer than broad; bristles over entire surface; with 3 pairs of sigilla (Figure 55), each pair increasing in size from anterior to posterior; posterior pair elongate and slightly curved; anterior pair located near edge of sternum.

Pedipalp: Tarsus with thick scopula.

Legs: Coxal cuspules absent (Figure 52). Scopula present on all tarsi, and metatarsi I and II. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 8.5. Leg II: femur 8.0. Leg III: Absent. Leg IV: femur 9.0.

Abdomen (Figures 56, 57): densely pilose. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Genitalia (Figures 58, 59): 2 pairs of spermathecae, median pair slightly coiled, lateral pair straight and with slightly bulbous head.

Dimensions (mm): Total body length ? (damaged); carapace length 11.2, width 9.4; sternum length 5.6, width 5.1; abdomen ? (damaged).

DISTRIBUTION

Aname lillianae is widely distributed throughout the northern wheatbelt of Western Australia, including the following IBRA regions: Avon Wheatbelt, Coolgardie, Murchison, and Yalgoo (Figure 151).

REMARKS

Most males were collected during the summer months of January to March, although one was collected in August. The sole female was collected from Tutanning Nature Reserve and is associated with this species based on the occurrence of a male from the same location and their overall similarity, especially in its large size and yellow-brown colouration which is a relatively uncommon pair of characteristics for *Aname* species in this region.

This species was formerly known by the WAM identification code *Aname* 'MYG522'.

SEQUENCE DATA

Molecular data are not available for this species.

ETYMOLOGY

This species is named for Lillian Huey, daughter of Joel A. Huey.

Aname mccleeryorum Harvey and Huey, sp. nov.

Figures 60–90

urn:lsid:zoobank.org:act:E9053B92-0DAD-400C-B965-5E3FA213FCB8

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** ♂, Chapman Valley, 28°30'S, 114°47'E, 1 April 2003, J. Webb (WAM T53979 DNA).

Paratypes

Australia: ***Western Australia:*** 1 ♂, Geraldton, David Road, 28°43'S, 114°39'E, 24 May 1995, R. McAlpine (WAM T32568); 1 ♀, Lesueur National Park, University Track, western end, 30°09'33"S, 115°12'14"E, 239 m, 6 December 2016, wandoo woodland, J.A. Huey, M. Hillyer, J. Carvajal, M.S. Harvey (WAM T142298 DNA); 1 ♀, Coorow-Green Head Road, 30°03'47"S, 115°10'44"E, 122 m, 7 December 2016, wandoo woodland, J. Carvajal, J.A. Huey, M. Hillyer, M.S. Harvey (WAM T142302 DNA).

Other material

Australia: ***Western Australia:*** 2 ♀, 2 penultimate ♂, Greenough, 28°57'S, 114°44'E, 13 January 1977, C.L. Duncan (WAM T27543–27546); 1 juvenile, Lesueur National Park, c. 380 m N. of University Track, 30°09'02"S, 115°14'09"E, 209 m, 5 December 2016, kwongan heath on sand, M.S. Harvey, J.A. Huey, M. Hillyer, J. Carvajal (WAM T142296 DNA); 1 juvenile, Lesueur National Park, 30°10'54"S, 115°15'01"E, 179 m, 6 December 2016, wandoo woodland, J. Carvajal, J.A. Huey, M. Hillyer, M.S. Harvey (WAM T142300 DNA); 1 ♀ (died in captivity, fragments only), same data (WAM T142299); 1 ♀, Oakajee, 28°34'19.45"S, 114°36'03.49"E, 1 August 2006, M. Davis, J. Clark (WAM T104747); 3 ♀, Oakajee, 28°34'24.78"S, 114°36'20.64"E, 1–5 August 2006, M. Davis, J. Clark (WAM T107695, T129049, T129050); 1 juvenile, Oakajee, 28°34'10.00"S, 114°36'15.00"E, 1–5 August 2006, M. Davis, J. Clark (WAM T107689).

DIAGNOSIS

Aname mccleeryorum most closely resembles *A. exulans* as the females have distinct chevron patterning on the abdomen, which is diffusely grey on a light background (Figures 85, 90) but with a dark median stripe and several indistinct chevrons in *A. exulans* (Figure 27). Males of *A. mccleeryorum* differ from *A. exulans* in the shape of the pedipalp including the shorter tibial depression and the shorter and slightly curved embolus (Figures 71–73). Females differ by short, slightly curved spermathecal lobes (Figures 87, 88) which are coiled and distally bifurcate in *A. exulans* (Figures 29–30).

DESCRIPTION

Male: based on holotype (WAM T53979)

Colour (in alcohol): Carapace deep brown; legs brown, some segments with longitudinal pale stripes, tarsi paler; chelicerae deep red-brown; abdomen dorsally grey-brown, and ventrally pale yellow-brown.

Cephalothorax: Carapace (Figure 60) 1.28 × longer than broad, pilose, silver hairs present, with brown bristles dorsally. Clypeal edge protruding medially. Fovea slightly procurved (Figure 62). Eyes on distinct mound (Figure 61); from above, anterior eye row straight, posterior eye row slightly recurved; AME about same size as ALE; ALE and AME the largest; PME smallest; eye group length 0.9, width 1.5. Chelicerae with short black setae, sparsely distributed, 1 well-defined prolateral strip of dense, long, and brown or black setae; rastellum absent; promargin of tooth row with 10 teeth, retromargin with 6 teeth. Labium fused to sternum (Figure 65); without cuspules. Maxillae (Figure 65) with 204 cuspules; located on basal third. Sternum (Figure 64): oval, posteriorly pointed; 1.23 × longer than broad; bristles over entire surface; with 3 pairs of sigilla (Figure 66), each pair increasing in size from anterior to posterior; posterior pair elongate and slightly curved; anterior and median pairs located near edge of sternum.

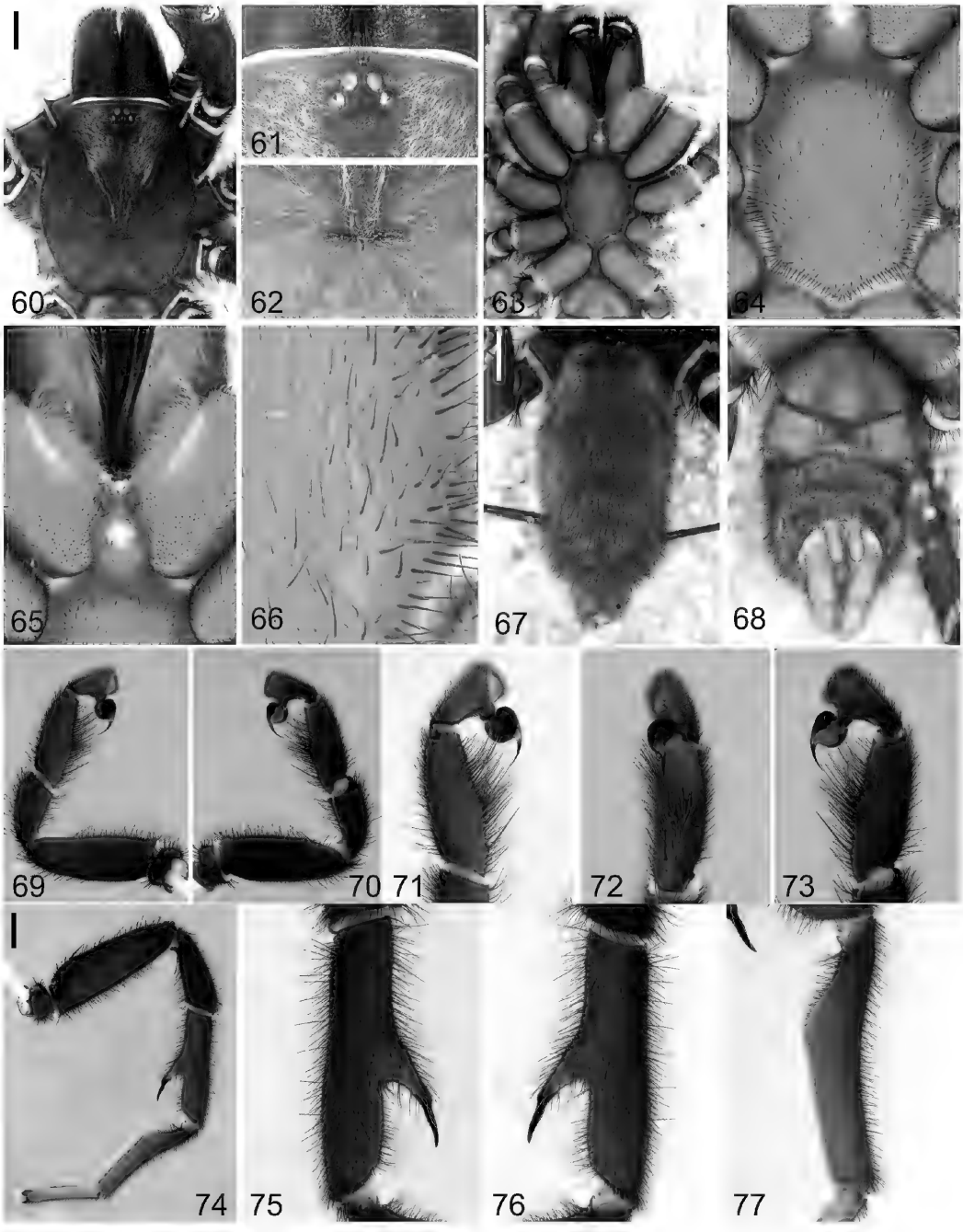
Pedipalp (Figures 69–73): Tibia cylindrical, narrow; asetose depression present, about the length of embolus; PDL/PTL 0.44. Tarsus short, broadest distally; densely setose; bulb globular; embolus short, not much longer than bulb, gently curved.

Legs: Coxal cuspules absent (Figure 63). Tibia I with large megaspur (Figures 74–76); TIL/TID 4.13; TIS/TIL 0.55; TISH/TID 0.79; metatarsus incrassate (Figure 77); MIL/MID 4.68; MIPEL/MIL 0.42. Scopula present on all tarsi, present on metatarsi I and II, present on distal half of metatarsi III and IV. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 8.5, tibia 8.8, metatarsus 7.2. Leg II: femur 8.0. Leg III: femur 5.8. Leg IV: femur 8.4.

Abdomen (Figures 67, 68): 1.9 × longer than broad, densely pilose. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Dimensions (mm): Total body length 24.7; carapace length 10.9, width 8.5; sternum length 5.3, width 4.3; abdomen length 8.8, width 4.7.

Variation: N = 1. Carapace length 11.1; width 8.5; femur I length 8.8; metatarsus I length 6.9; femur IV length 8.6.

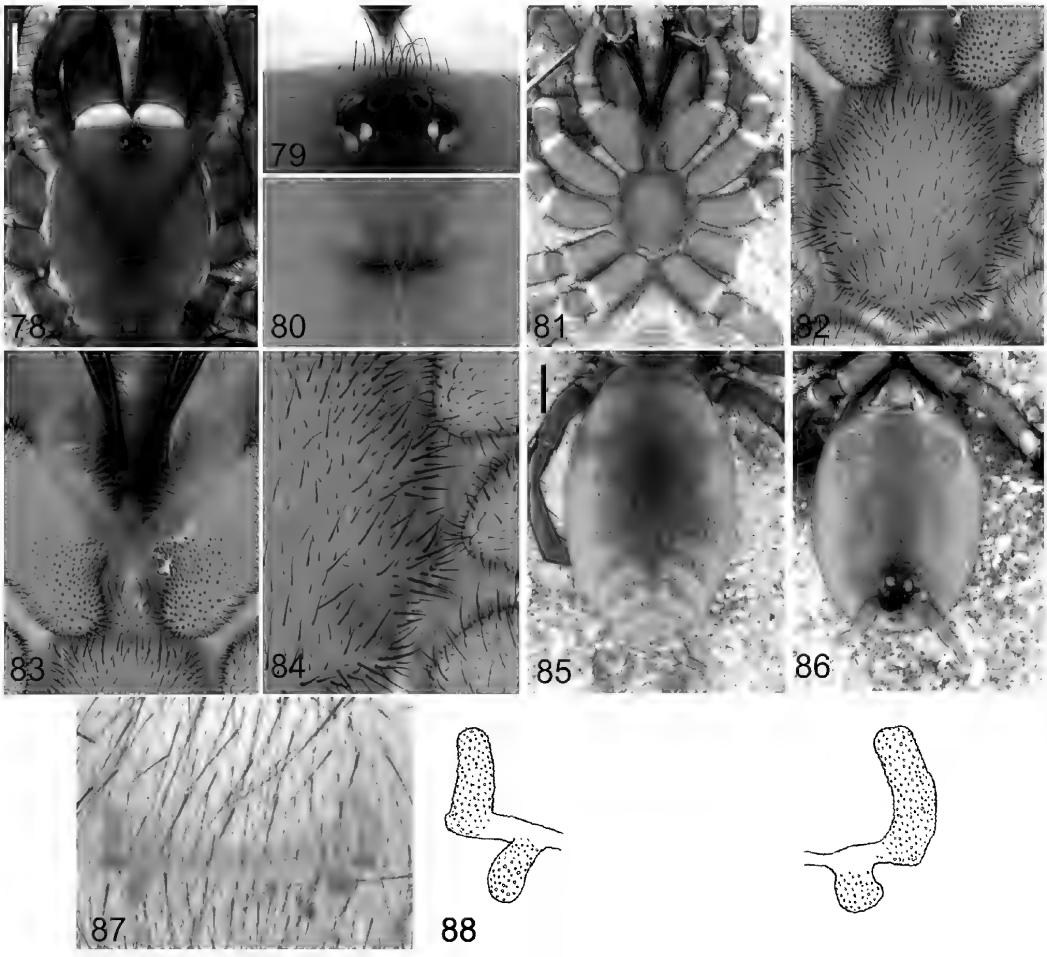


FIGURES 60–77 *Aname mccleeryorum* sp. nov., holotype male (WAM T53979): 60) cephalothorax, dorsal view; 61) ocular region; 62) fovea; 63) cephalothorax, ventral view; 64) sternum, ventral view; 65) maxillae and labium, ventral view; 66) left sigilla, ventral view; 67) abdomen, dorsal view; 68) abdomen, ventral view; 69) left pedipalp, prolateral view; 70) left pedipalp, retrolateral view; 71) left pedipalp, tibia and tarsus, prolateral view; 72) left pedipalp, tibia and tarsus, ventral view; 73) left pedipalp, tibia and tarsus, retrolateral view; 74) left leg I, prolateral view; 75) left leg I, tibia I, retrolateral view; 76) left leg I, tibia I, prolateral view; 77) left leg I, metatarsus I, prolateral view. Scale lines = 2 mm.

Female: based on paratype (WAM T142298)

Colour (in alcohol): Carapace pale brown, with darker V-shaped marking delineating cephalic region; legs brown, some segments with longitudinal pale stripes, tarsi paler; chelicerae deep red-brown; abdomen dorsally base colour grey, with darker grey antero-dorsal patch and several posterior chevrons, and ventrally pale yellow-brown.

Cephalothorax: Carapace (Figure 78) 1.22 × longer than broad; with sparse fine setae, silver hairs sparsely present, with brown bristles dorsally. Clypeal edge protruding medially. Fovea slightly procurved (Figure 80). Eyes on distinct mound (Figure 79); from above, anterior eye row straight, posterior eye row slightly recurved; AME about same size as ALE; ALE and AME the largest; PME smallest; eye group length 0.8, width 1.4. Chelicerae with short black setae, sparsely distributed, 1 well-defined prolateral strip of dense, long, and brown or black setae; rastellum absent; promargin of tooth row with 9 teeth, retromargin with 7 teeth. Labium fused to sternum (Figure 83); without cuspules. Maxillae (Figure 83) with c. 155 cuspules; located on basal third. Sternum (Figure 82): oval, posteriorly pointed; 1.19 × longer than broad; bristles over entire surface; with 3 pairs of sigilla (Figure 84), each pair increasing in size from anterior to posterior; posterior pair elongate and slightly curved; anterior and median pairs located near edge of sternum.



FIGURES 78–88 *Aname mccleeryorum* sp. nov., paratype female (WAM T142298): 78) cephalothorax, dorsal view; 79) ocular region; 80) fovea; 81) cephalothorax, ventral view; 82) sternum, ventral view; 83) maxillae and labium, ventral view; 84) left sigilla, ventral view; 85) abdomen, dorsal view; 86) abdomen, ventral view; 87) spermathecae, dorsal view; 88) spermathecae, dorsal view, line drawing. Scale lines = 2 mm.

FIGURES 89–90 *Aname mccleeryorum* sp. nov., paratype juvenile (WAM T142296): 89) lateral view; 90) posterior view.

Pedipalp: Tarsus with thick scopula.

Legs: Coxal cuspules absent (Figure 81). Scopula present on all tarsi, present on metatarsi I and II, present on distal half of metatarsi III and IV. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 6.1. Leg II: femur 5.5. Leg III: femur 5.1. Leg IV: femur 6.1.

Abdomen (Figures 85, 86): 1.5 × longer than broad, sparsely setose. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Genitalia (Figures 87, 88): Spermathecal lobes short, gently curved.

Dimensions (mm): Total body length 28.5; carapace length 8.4, width 6.9; sternum length 4.3, width 3.6; abdomen length 10.9, width 7.3.

Variation: N = 3; carapace length 10.2–12.2, width 8.2–8.7; femur I length 6.4–8.1; femur IV length 7.3–7.9.

DISTRIBUTION

Aname mccleeryorum has been found throughout the Geraldton Sandplains IBRA bioregion of Western Australia, from Oakajee and Chapman Valley south to Lesueur National Park (Figure 151).

REMARKS

The male holotype of *A. mccleeryorum* was matched to some of the adult females using sequence data (Figure 1). The two males were collected in autumn (April and May).

This species was formerly known by the WAM identification code *Aname* 'MYG632'.

SEQUENCE DATA

Within-species genetic divergence for *A. mcleeryorum* was 2.7% at *COI*, suggesting some population genetic structure across its range. It is closely related to *A. exulans* (7.5%), which is found on the neighbouring offshore Houtman Abrolhos islands (Figure 151).

ETYMOLOGY

This species is named for the McCleery family, in recognition of their generous support for the Foundation of the Western Australian Museum.

Aname phillipae Harvey and Huey, sp. nov.

Figures 91–119

urn:lsid:zoobank.org:act:37FB4C77-4E16-4F80-A652-BD4B476E2FF8

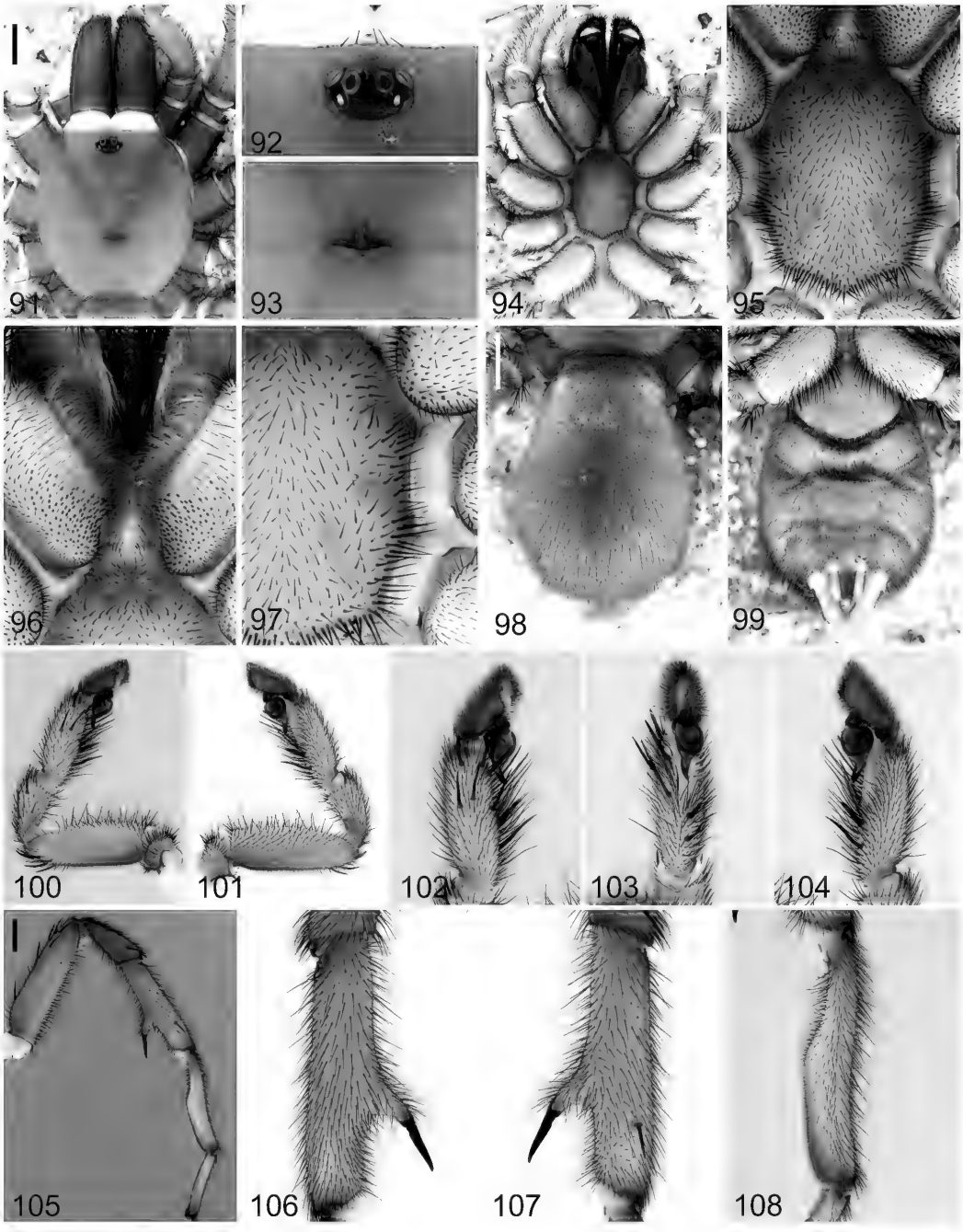
MATERIAL EXAMINED

Holotype

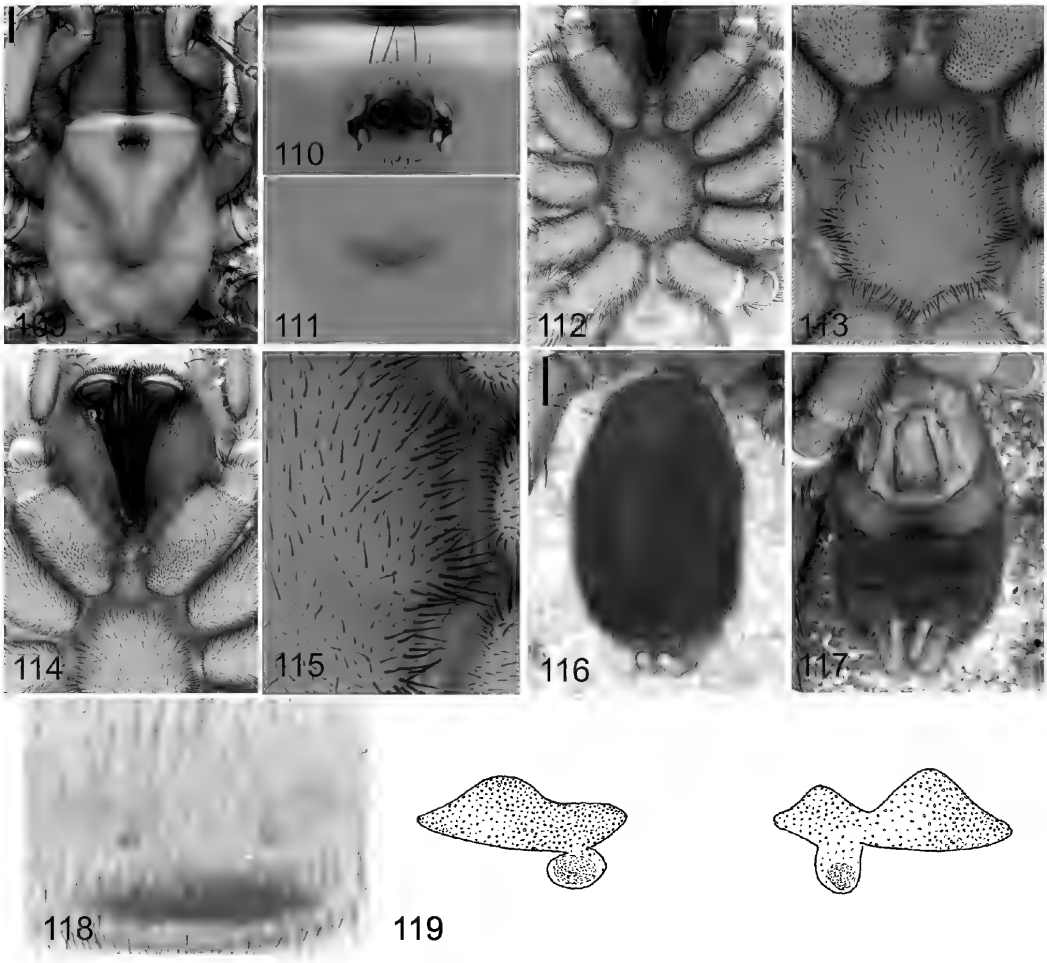
Australia: ***Western Australia:*** ♂, Deception Hill, 111.15 km NNW. of Koolyanobbing, 29°51'56"S, 119°16'37"E, 7 December 2010, dry pitfall trap, R. Teale, Z. Hamilton, V. Cartledge (WAM T110142[DNA]).

Paratypes

Australia: ***Western Australia:*** 1 ♂, Deception Hill, 93.10 km NNW. of Koolyanobbing, 30°02'06"S, 119°16'28"E, 7 December 2010, dry pitfall trap, R. Teale, Z. Hamilton, V. Cartledge (WAM T109203 [DNA]); 1 ♂, Windarling Mine Lease (Portmans), c. 27 km N. of Mt Jackson, 30°00'36.3"S, 119°16'27.0"E, 30 November 2006, dry pitfall trap, open mulga woodland, B.M. Metcalf (WAM T132579); 1 ♀, S. of Kambalda, 31°34'03"S, 121°44'42"E, April 2006, S. Thompson (WAM T95772 [DNA]).



FIGURES 91–108 *Aname phillipae* sp. nov., holotype male (WAM T110142): 91) cephalothorax, dorsal view; 92) ocular region; 93) fovea; 94) cephalothorax, ventral view; 95) sternum, ventral view; 96) maxillae and labium, ventral view; 97) left sigilla, ventral view; 98) abdomen, dorsal view; 99) abdomen, ventral view; 100) left pedipalp, prolateral view; 101) left pedipalp, retrolateral view; 102) left pedipalp, tibia and tarsus, prolateral view; 103) left pedipalp, tibia and tarsus, ventral view; 104) left pedipalp, tibia and tarsus, retrolateral view; 105) left leg I, prolateral view; 106) left leg I, tibia I, retrolateral view; 107) left leg I, tibia I, prolateral view; 108) left leg I, metatarsus I, prolateral view. Scale lines = 2 mm.



FIGURES 109–119 *Aname phillipae* sp. nov., paratype female (WAM T95772): 109) cephalothorax, dorsal view; 110) ocular region; 111) fovea; 112) cephalothorax, ventral view; 113) sternum, ventral view; 114) maxillae and labium, ventral view; 115) left sigilla, ventral view; 116) abdomen, dorsal view; 117) abdomen, ventral view; 118) spermathecae, dorsal view; 119) spermathecae, dorsal view, line drawing. Scale lines = 2 mm.

Other material

Australia: ***Western Australia:*** 1 ♂, Bungalbin Hill, 48.2 km NNE. of Koolyanobbing, 30°17'38.34"S, 119°25'30.84"E, 12–25 December 2012, S. White (WAM T127943); 7 ♂, Lord Nelson [mine], 10.3 km SSW. of Black Hill, site LN03, 28°09'36"S, 119°30'36"E, 25 October 2004, dry pitfall trap, M. Craig (WAM T64911–64916 [DNA], T72397); 1 ♂, Lorna Glen Station, quadrat 24, 26°07'49"S, 121°31'02"E, 25 November–1 December 2004, dry pitfall, M.A. Cowan et al. (WAM T66411); 1 ♂, Mt Forrest, c. 27 km SE. of Bulga Downs Homestead, 28°41'46"S, 119°56'35"E, 12 December 2012, dry pitfall trap, open mulga woodland over open shrubland on plain, G.P. Harewood, G. Murray (WAM T128129); 1 ♂, Mt Ida, 80 km NW. of Menzies, 29°11'01"S, 120°25'18"E, 26 October 2011, pitfall trap, *Eucalyptus* woodland, V. Saffer (WAM T121519 [DNA]).

DIAGNOSIS

Aname phillipae most closely resembles *A. whitei*, *A. lillianae* and *A. simoneae*, as adults of all three species are large and rather pale, with extremely narrow third sigilla (Figures 97, 115). Males are most similar to *A. whitei* and *A. simoneae* as the embolus is thickened and flattened (Figure 102–104) but *A. phillipae* differs from all these species by the embolic tip being noticeably hooked (Figure 103). The female spermathecae, which consist of a low, rounded basal section with a medial anteriorly directed spermatheca with a bulbous distal

end (Figures 118, 119), cannot be distinguished from those of *A. whitei* and *A. simoneae*, but differ from those of *A. lillianae* which consist of two pairs of long spermathecae of which the median pair are slightly coiled (Figure 59).

DESCRIPTION

Male: based on holotype (WAM T110142)

Colour (in alcohol): Carapace cephalic region deep red-brown, thoracic region yellow-brown; leg I red-brown, legs II to IV uniformly yellow-brown; chelicerae uniformly dark red-brown; abdomen grey-brown.

Cephalothorax: Carapace (Figure 91) 1.11 × longer than broad; with sparse fine setae, silver hairs present, with brown bristles dorsally. Clypeal edge straight. Fovea slightly procurved (Figure 93). Eyes (Figure 92) on distinct mound; from above, anterior eye row straight, posterior eye row slightly recurved; AME about same size as ALE; ALE and AME the largest; PME smallest; eye group length 0.82, width 1.01. Chelicerae with broad dorsal strip of black setae, and 2 thinner lateral strips of smaller black setae; rastellum absent; promargin of tooth row with 10 teeth, retromargin with 4 teeth. Labium fused to sternum (Figure 96); without cuspules. Maxillae (Figure 96) with 112 cuspules; located on basal half. Sternum (Figure 95): oval, posteriorly pointed; 1.18 × longer than broad; bristles over entire surface. With 3 pairs of very faint sigilla (Figure 97); each pair increasing in size from anterior to posterior; posterior pair elongate and slightly curved.

Pedipalp (Figures 100 104): Tibia cylindrical, narrow; asetose depression present, about the length of embolus; PDL/PTL 0.49. Tarsus short, broadest distally; densely setose; bulb ovoid; embolus shorter than bulb, flattened, terminating in constricted and slightly hooked tip.

Legs: Coxa I with 2–3 cuspules near medial edge of coxa I (Figures 94, 95). Tibia I with large megaspur (Figures 105–107); TIL/TID 4.11; TIS/TIL 0.62; TISH/TID 0.71; metatarsus incrassate (Figure 108); MIL/MID 5.04; MIPEL/MIL 0.52. Scopula present on tarsi and metatarsi of all legs. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 8.5, tibia 8.4, metatarsus 6.4. Leg II: femur 7.9. Leg III: femur 6.7. Leg IV: femur 8.5.

Abdomen (Figures 98, 99): 1.4 × longer than broad, densely pilose. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Dimensions (mm): Total body length 18.4; carapace length 8.8, width 7.9; sternum length 4.5, width 3.8; abdomen length 9.2, width 6.4.

Variation: N = 10; carapace length 8.2–9.4; width 7.5–8.2; femur I length 7.3–8.7; metatarsus I length 5.7–6.7; femur IV length 8.2–9.6.

Female: based on paratype (WAM T95772)

Colour (in alcohol): Carapace anterior brown-yellow fading to yellow-brown posteriorly; legs uniformly red-brown; chelicerae yellow-brown; abdomen grey-brown.

Cephalothorax: Carapace (Figure 109) 1.19 × longer than broad; with sparse fine setae, silver hairs absent, with brown bristles dorsally. Clypeal edge protruding medially. Fovea slightly procurved (Figure 111). Eyes on distinct mound (Figure 110); from above, anterior eye row slightly procurved, posterior eye row slightly recurved; AME larger than ALE; ALE largest; PME smallest; eye group length 0.96, width 1.88. Chelicerae with short black setae, sparsely distributed, with 1 well-defined prolateral strip dense, long, and brown or black setae; rastellum absent; promargin of tooth row with 10 teeth, retromargin with 4 teeth. Labium fused to sternum (Figure 114); with 1 cuspule. With c. 210 cuspules; located in basal half. Sternum (Figure 113): oval, posteriorly pointed; 1.14 × longer than broad; bristles over entire surface; with 3 pairs of sigilla (Figure 115), each pair increasing in size from anterior to posterior; anterior pair located near edge of sternum; posterior pair elliptical.

Pedipalp: Tarsus with thick scopula.

Legs: Coxal cuspules absent (Figure 112). Scopula present on all tarsi, present on metatarsi I and II, present on distal half of metatarsi III and IV. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 9.2. Leg II: femur 8.2. Leg III: femur 7.3. Leg IV: femur 9.4.

Abdomen (Figures 116, 117): 1.4 × longer than broad, densely pilose. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Genitalia (Figures 118, 119): Low, rounded basal section with medial anteriorly directed spermatheca, with bulbous distal end.

Dimensions (mm): Total body length 25; carapace length 11.6, width 9.8; sternum length 5.8, width 5.1; abdomen length 10.9, width 7.7.

DISTRIBUTION

Aname phillipae has been found in the Gascoyne, Murchison and Coolgardie IBRA bioregions of Western Australia (Figure 151).

REMARKS

The female was matched with the males using sequence data (Figure 1). Males have been collected in pitfall traps during the spring and summer months of October to December.

This species was formerly known by the WAM identification code *Aname* 'MYG604'.

SEQUENCE DATA

Despite showing significant genetic structure in the concatenated phylogeny (Figure 1), only one specimen was successfully sequenced at *COI*. This genetic structure was primarily based on structure in 16S (data not shown). *Aname phillipae* is closely related to *A. simoneae* and *A. whitei*, to which it is very similar morphologically.

ETYMOLOGY

This species is named for Phillipa Huey, daughter of Joel A. Huey.

Aname simoneae Harvey and Huey, sp. nov.

Figures 120–150

urn:lsid:zoobank.org:act:C2D21926-A117-468F-A25A-6EC0E01CED4E

Aname MY2121: Hedin and Bond 2006: figs 4, 5; Bond et al. 2012: figs 1, 2; Wheeler et al. 2017: fig. 2; Opatova et al. 2020: fig. 3 (which states 'MY2131').

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** ♂, 21 km S. of Laverton, 28°47'34"S, 122°25'53"E, 8 January 2011, pit trap, S.A. Thompson (WAM T110261[DNA]).

Paratypes

Australia: ***Western Australia:*** 1 ♂, Lake Way, 15 km SSE. of Wiluna, 26°50'33"S, 120°21'47"E, 10 March 2010, P. Bolton (WAM T101218); 1 ♀, same data except 24 October 2007 (WAM T104712); 1 ♀, c. 41.5 km SSE. of Menzies, 30°04'21.91"S, 121°10'35.75"E, 4 May 2018, dug from burrow, E.S. Volschenk (WAM T149148[DNA]).

Other material

Australia: ***Western Australia:*** 2 ♂, Black Swan Nickel Mine, 50 km NE. of Kalgoorlie, 30°23'54"S, 121°40'53"E, 12 December 2003–5 January 2004, pitfall trap, P.R. Langlands (WAM T56915); 1 ♂, Bulong, 30°45'S, 121°48'E, 1 December 1932, F. Jones (WAM T2500, formerly 32/2686); 2 ♂, Goldminer Caravan Park, Kalgoorlie, 30°44'S, 121°28'E, 20 January 1993, G. Thompson (WAM T27289–27290, formerly 93/605–606); 1 ♂, Mt Vetters Station, Black Swan Nickel Mine, 50 km NE. of Kalgoorlie, 30°23'56"S, 121°41'06"E, 12 December 2003, 5 January 2004, pitfall trap, P.R. Langlands (WAM T56960); 3 ♂, Ora Banda, 30°23'S, 121°04'E, January 2006, S. Thompson (WAM T95768); 1 ♂, 7–8 km WNW. of Point Salvation, red sands site, 28°12'S, 123°36'E, 27 December 1995, pitfall trap, E.R. Pianka (WAM T44223); 1 juvenile, Wanjarri, 53.3 km S. of Lake Way homestead, site YAK07B, 27°24'24"S, 120°36'42"E, dug from burrow, 4 December 2005, R. Teale (WAM T76834[DNA]).

DIAGNOSIS

Aname simoneae most closely resembles *A. whitei*, *A. lillianae* and *A. phillipae* as adults of all three species are large and rather pale, with extremely narrow third sigilla (Figures 97, 115). Males are most similar to *A. whitei* and *A. phillipae* as the embolus is thickened and flattened (Figures 131–133) but differ from *A. phillipae* by the lack of distinct terminal hook and from *A. whitei* by the shape of the embolus which is more evenly tapered. The embolus of *A. lillianae* is slender and tapering. The female spermathecae, which consist of a low, rounded basal section with a medial anteriorly directed spermatheca with a bulbous distal end (Figures 147, 148), cannot be distinguished from those of *A. whitei* and *A. phillipae*, but differ from those of *A. lillianae* which consist of two pairs of long spermathecae of which the median pair are slightly coiled (Figure 59).

DESCRIPTION

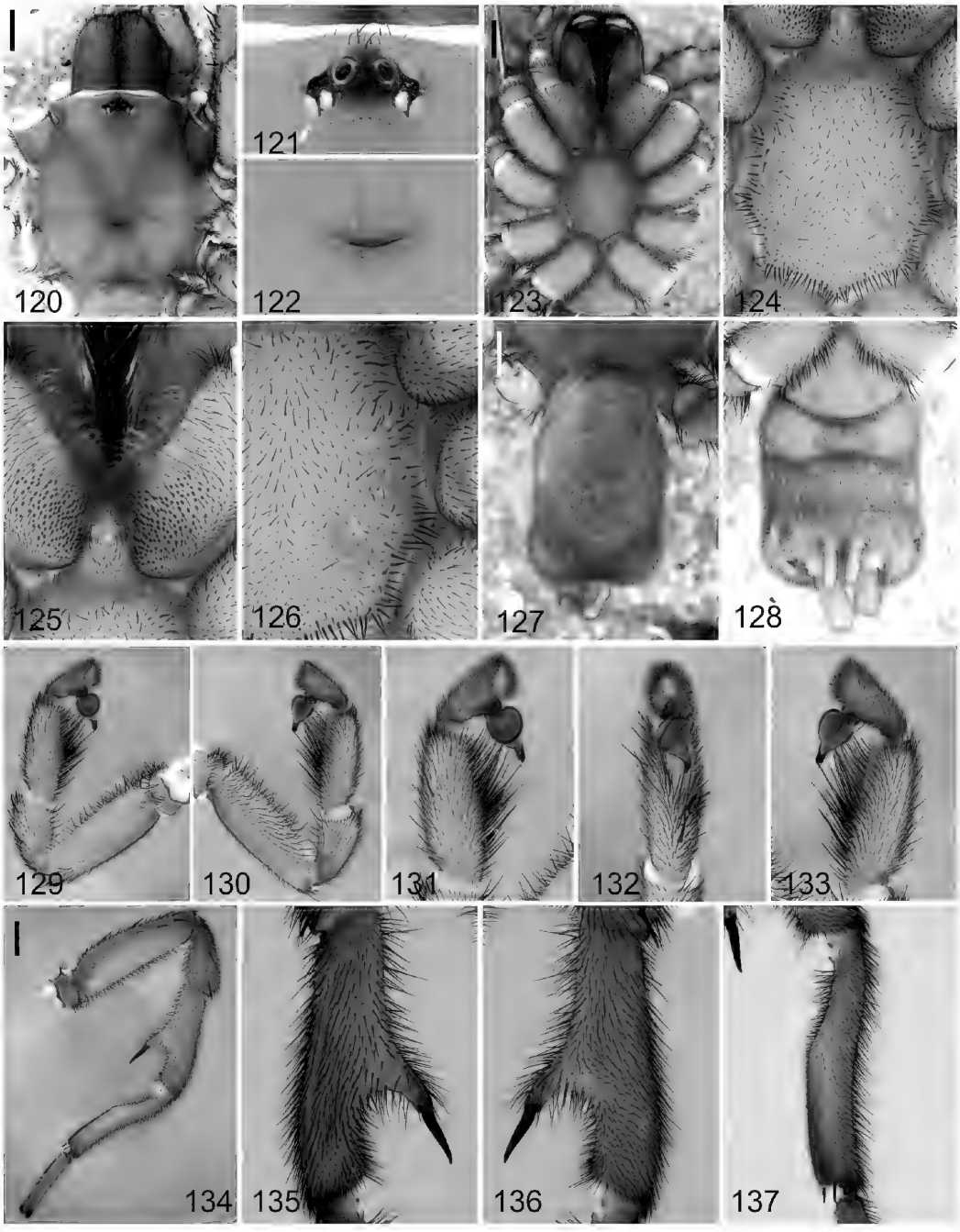
Male: based on holotype (WAM T110261)

Colour (in alcohol): Carapace anterior light orange-brown fading posteriorly to pale yellow; leg I red-brown, legs II to IV uniformly yellow-brown; chelicerae burnt orange; abdomen dorsally pale creamy-yellow, and ventrally pale creamy-yellow.

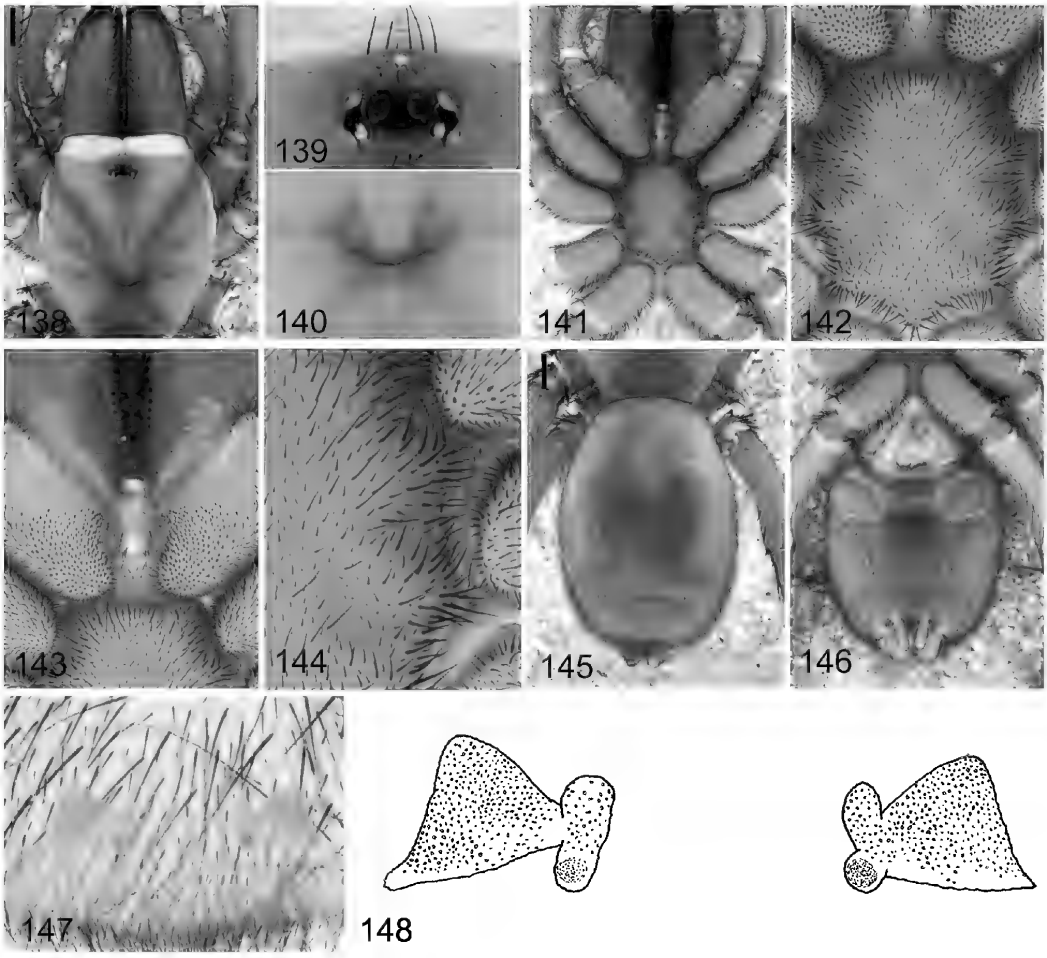
Cephalothorax: Carapace (Figure 120) 1.22 × longer than broad; with sparse short setae, silver hairs absent; without dorsal bristles. Clypeal edge straight. Fovea slightly procurved (Figure 122). Eyes on distinct mound (Figure 121); from above, anterior eye row procurved, posterior eye row nearly straight; AME larger than ALE; ALE largest; PME smallest; eye group length 0.96, width 1.58. Chelicerae with short black setae, sparsely distributed; with 1 well-defined prolateral strip of dense, long, and brown or black setae; rastellum absent; promargin of tooth row with 10 teeth, retromargin with 4 or 5 teeth. Labium fused to sternum (Figure 125); without cuspules. Maxillae (Figure 125) with c. 134 cuspules; located on basal half. Sternum (Figure 124): oval, posteriorly pointed; 1.18 × longer than broad; bristles over entire surface; with 3 pairs of sigilla (Figure 126), each pair increasing in size from anterior to posterior; anterior pair located near edge of sternum; posterior pair elliptical.

Pedipalp (Figures 129–133): Tibia cylindrical, narrow; asetose depression present, about the length of embolus; PDL/PTL 0.39; densely setose; bulb ovoid; embolus shorter than bulb, flattened, terminating in constricted tip.

Legs: Coxal cuspules absent (Figure 123). Tibia I with large megaspur (Figures 134–136); TIL/TID 4.58; TIS/TIL 0.61; TISH/TID 1.08; metatarsus slightly incrassate (Figure 137); MIL/MID 5.24; MIPEL/MIL 0.48.



FIGURES 120–137 *Aname simoneae* sp. nov., holotype male (WAM T110261): 120) cephalothorax, dorsal view; 121) ocular region; 122) fovea; 123) cephalothorax, ventral view; 124) sternum, ventral view; 125) maxillae and labium, ventral view; 126) left sigilla, ventral view; 127) abdomen, dorsal view; 128) abdomen, ventral view; 129) left pedipalp, prolateral view; 130) left pedipalp, retrolateral view; 131) left pedipalp, tibia and tarsus, prolateral view; 132) left pedipalp, tibia and tarsus, ventral view; 133) left pedipalp, tibia and tarsus, retrolateral view; 134) left leg I, prolateral view; 135) left leg I, tibia I, retrolateral view; 136) left leg I, tibia I, prolateral view; 137) left leg I, metatarsus I, prolateral view. Scale lines = 2 mm.



FIGURES 138–148 *Aname simoneae* sp. nov., paratype female (WAM T149148): 138) cephalothorax, dorsal view; 139) ocular region; 140) fovea; 141) cephalothorax, ventral view; 142) sternum, ventral view; 143) maxillae and labium, ventral view; 144) left sigilla, ventral view; 145) abdomen, dorsal view; 146) abdomen, ventral view; 147) spermathecae, dorsal view; 148) spermathecae, dorsal view, line drawing. Scale lines = 2 mm.

Scopula present on all tarsi, and metatarsi I and II. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 8.1, tibia 8.5, metatarsus 7.2. Leg II: femur 7.8. Leg III: femur 7.0. Leg IV: femur 7.7.

Abdomen (Figures 127, 128): 1.6 × longer than broad, densely pilose. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

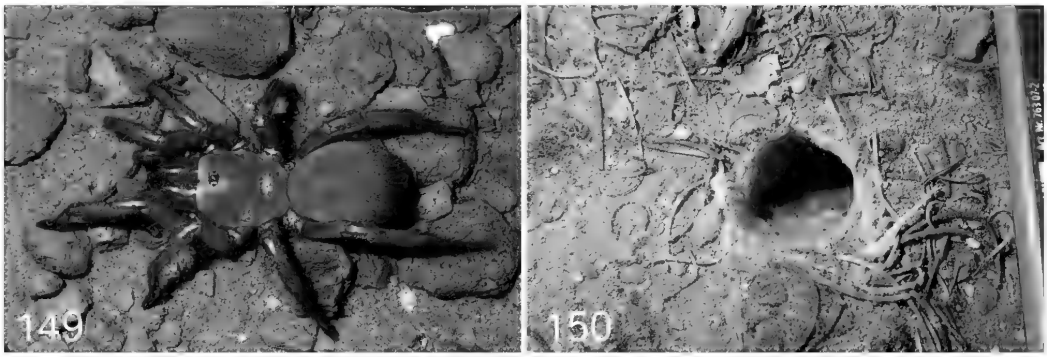
Dimensions (mm): Total body length 24.0; carapace length 9.8, width 8.0; sternum length 4.8, width 4.1; abdomen length 9.4, width 5.8.

Variation: N = 10; carapace length 9.3–13.3; width 8.1–10.1; femur I length 8.4–9.7; metatarsus I length 7.1–7.7; femur IV length 9.1–10.2.

Female: based on paratype (WAM T149148)

Colour (in alcohol): Carapace dark yellow-brown with red-brown radial markings; legs uniformly red-brown; chelicerae uniformly dark red-brown; abdomen grey-brown.

Cephalothorax: Carapace (Figure 138) 1.04 × longer than broad; with sparse fine setae, silver hairs absent, with brown bristles dorsally. Clypeal edge protruding medially. Fovea slightly procurved (Figure 140). Eyes on distinct mound (Figure 139); from above, anterior eye row slightly procurved, posterior eye row slightly



FIGURES 149–150 *Aname simoneae* sp. nov., paratype female (WAM T149148): 149, dorsal view; 150, burrow entrance. (Image courtesy Erich Volschenk.)

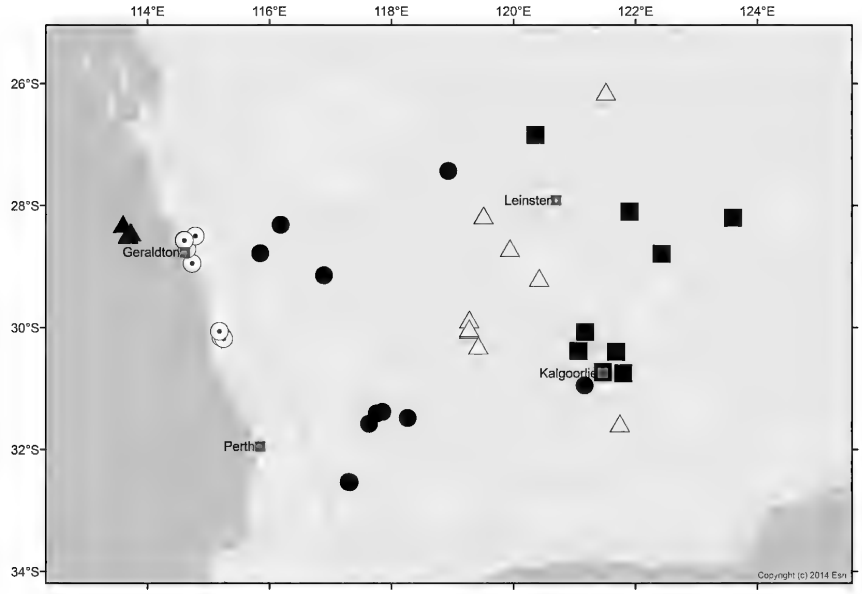
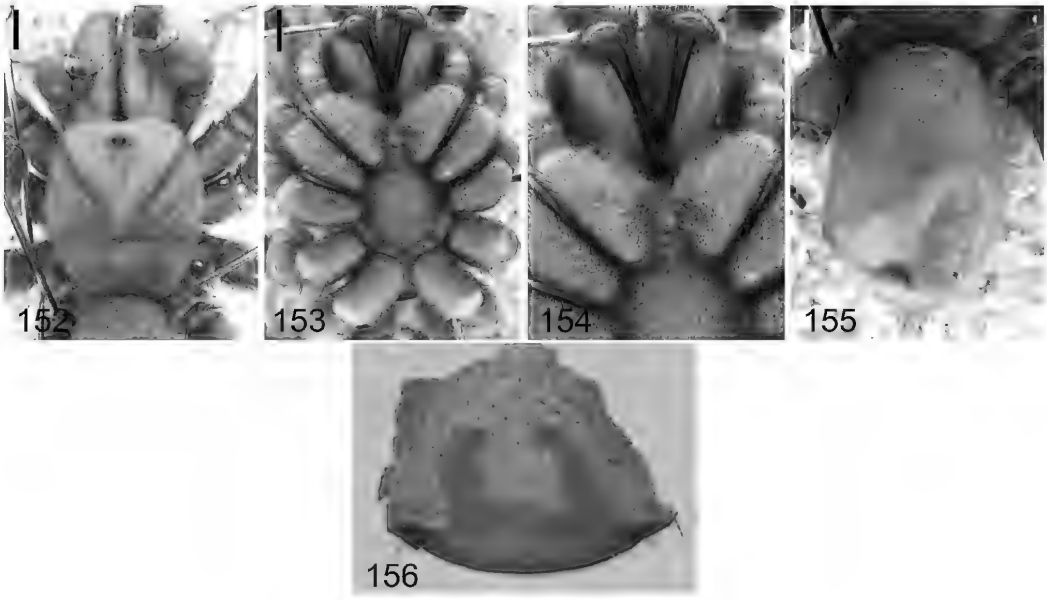


FIGURE 151 Known distributions of the *Aname* species treated in this paper, superimposed over IBRA bioregions: *Aname exulans* sp. nov. (solid triangle); *A. lillianae* sp. nov. (solid circle); *A. mccleeryorum* sp. nov. (open circle); *A. phillipae* sp. nov. (open triangle); *A. simoneae* sp. nov. (solid square).

recurved; AME about same size as ALE; ALE and AME the largest; PME smallest; eye group length 1.0, width 1.8. Chelicerae with broad dorsal strip of black setae, and two thinner lateral strips of smaller black setae; rastellum absent; promargin of tooth row with 11 teeth, retromargin with 5 teeth. Labium fused to sternum (Figure 143); without cuspules. Maxilla (Figure 143) with c. 215 cuspules; located on basal half. Sternum (Figure 142): oval, posteriorly pointed; 1.2 × longer than broad; bristles over entire surface; with 3 pairs of sigilla (Figure 144), each pair increasing in size from anterior to posterior; anterior pair located near edge of sternum; posterior pair elongate.

Pedipalp: Tarsus with thick scopula.

Legs: Coxal cuspules absent (Figure 141). Scopula present on all tarsi, present on metatarsi I and II. Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 8.9. Leg II: femur 8.1. Leg III: femur 7.2. Leg IV: femur 9.3.



FIGURES 152–156 *Proshermacha armigera*, holotype female (AM KS8193): 152) cephalothorax, dorsal view; 153) cephalothorax, ventral view; 154) maxillae, labium and sternum, ventral view; 155) abdomen, dorsal view; 156) spermathecae, dorsal view. Scale lines = 2 mm.

Abdomen (Figures 145, 146): 1.5 × longer than broad, densely pilose. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Genitalia (Figures 147, 148): Low, rounded basal section with medial anteriorly directed spermatheca, with bulbous distal end.

Dimensions (mm): Total body length 24.0; carapace length 9.9, width 9.5; sternum length 6.0, width 5.0; abdomen length 15.5, width 10.7.

Variation: N = 1; carapace length 10.6, width 8.3; femur I length 7.8; femur IV length 8.5.

DISTRIBUTION

Aname simoneae has been found in the Coolgardie, Great Victoria Desert and Murchison IBRA bioregions of Western Australia (Figure 151).

REMARKS

The female used for the description was matched with the male holotype using sequence data (Figure 1). The other female was collected from the same locality as a male. Males have been collected in pitfall traps during the summer months of December to March.

Our sequence data matched those of a specimen identified as *Aname* MY2121 in previous studies examining mygalomorph spider phylogenetics (Bond et al. 2012; Hedin and Bond 2006; Wheeler et al. 2017), and we are confident that this sample represents *A. simoneae*. Although the locality was given as 'N of Leonora S28.10172 E125.90417' by Hedin and Bond (2006), the site is actually located at S28.10172 E121.90417 (M. Hedin, in litt.).

This species was formerly known by the WAM identification code *Aname* 'MYG523'.

SEQUENCE DATA

Intraspecific genetic distances are high within *A. simoneae* (8.98%). *Aname simoneae* is closely related to *A. phillipae* and *A. whitei*, to which it is very similar morphologically.

ETYMOLOGY

This species is named for Simone Huey, wife of Joel A. Huey.

Genus *Proshermacha* Simon, 1908

Proshermacha Simon, 1908: 363. Type species: *Proshermacha subarmata* Simon, 1908, by subsequent designation of Rainbow (1911).

REMARKS

The genus *Proshermacha* was recently reinstated by Harvey et al. (2018) for a group of species from southern Australia that could be best diagnosed by characters found in the male pedipalp. Although the genus contains eight species, numerous new species have been observed in museum collections (Harvey et al. 2018).

Proshermacha armigera (Rainbow and Pulleine, 1918) comb. nov.,

Figures 152–156

urn:lsid:zoobank.org:act:47ECBBF8-E50F-401F-9E49-F066921C163E

Aname armigera Rainbow and Pulleine, 1918: 150, plate 23, figs 102, 103.

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** ♀, Mullewa [as 'Mullawa' (sic)] [28°32'S, 115°31'E], date unknown, F. May (AM KS8193).

DESCRIPTION

Female: based on holotype (AM KS8193)

Colour (in alcohol): Carapace uniformly yellow-brown; indeterminate (faded); chelicerae yellow-brown; abdomen dorsally grey-brown, and ventrally pale yellow-brown.

Cephalothorax: Carapace (Figure 152) 1.14 × longer than broad, densely pilose, silver hairs present, with brown bristles dorsally. Clypeal edge protruding medially. Fovea slightly procurved (Figure 154). Eyes on distinct mound (Figure 153); from above, anterior eye row straight, posterior eye row slightly recurved; AME larger than ALE; ALE and AME the largest; PME smallest; eye group length 0.6, width 1.4. Chelicerae with 2 well-defined rows of short black spines; rastellum absent; promargin of tooth row with 8 teeth, retromargin with 10 teeth. Labium fused to sternum (Figure 154); with 3 cuspules. Maxilla with c. 100 cuspules; located on the proximo-basal edge (Figure 154). Sternum (Figure 153): oval, posteriorly pointed; 1.16 × longer than broad; bristles over entire surface; with 3 pairs of sigilla (Figure 153), each pair increasing in size from anterior to posterior; anterior and median pairs located near edge of sternum.

Pedipalp: Tarsus densely setose.

Legs: Coxal cuspules absent (Figure 153). Trichobothria: tibia with numerous trichobothria in 2 rows, metatarsi with several trichobothria, tarsi with numerous trichobothria. Claws with 2 rows of teeth; claw tufts absent. Measurements: Leg I: femur 8.8. Leg II: femur 6.4. Leg III: femur 4.5. Leg IV: femur 6.9.

Abdomen (Figure 155): 1.4 × longer than broad, densely pilose with bristles. Spinnerets: 2 pairs of spinnerets; PMS unsegmented and separated by about diameter of spinneret; PLS 3-segmented, apical segment elongate, digitiform.

Genitalia (Figure 156): 1 pair of widely spaced, thickened, anteriorly directed spermathecae.

Dimensions (mm): Total body length 21.1; carapace length 8.3, width 7.3; sternum length 4.3, width 3.7; abdomen length 8.7, width 6.2.

DISTRIBUTION

Proshermacha armigera is known only from the holotype collected from Mullewa in the northern section of the Avon Wheatbelt IBRA region, Western Australia.

REMARKS

The original description of *A. armigera* was based on a single female collected from Mullewa in the north-western Wheatbelt region of Western Australia, although the locality was incorrectly stated to be 'Mullawa' (Rainbow and Pulleine 1918). The holotype is in fair condition, but many of the legs have become separated from the body.

As stated above, *Proshermacha* is best diagnosed by a combination of features found in males, including the presence of a large ventral tibial spur on leg I, the lack of a ventral asetose depression on the male pedipalpal tibia, the long embolus, and the lack of thickened setae on the retrolateral face of the male pedipalpal tibia, which renders the placement of the female holotype of *A. armigera* slightly problematic. The maxillary cuspules are restricted to the baso-mesal edge of the maxillae (Figure 154), which excludes it from *Aname* where the cuspules are spread over the entire basal half of the maxilla (Harvey et al. 2018). The restricted conformation is only known from species of *Chenistonia*, *Proshermacha* and *Teyl*, at least among the Western Australian anamid fauna. The general body plan does not resemble species of *Teyl* which tend to have gracile legs and rounded abdomens. Species of *Chenistonia* have only been recorded from mesic regions of southern Western Australia and have never been found in the mid-west region (MSH, JAH, unpublished data). Therefore, we here transfer *A. armigera* to the genus *Proshermacha* which have similarly shaped spermathecae (Harvey et al. 2018, figure 7G). There are no obvious morphological features that would help to distinguish *P. armigera* from others in the genus, and we have not been able to match the female with males of *Proshermacha* collected in the general vicinity of the type locality.

SEQUENCE DATA

Molecular data are not available for this species.

ACKNOWLEDGEMENTS

We are very grateful to Graham Milledge (Australian Museum, Sydney) for kindly lending the holotype of *Aname armigera*, and Erich Volschenk for supplying images and sequence data for a female of *Aname simoneae*. Part of this study was funded by the Gorgon Barrow Island Net Conservation Benefits Fund. The Fund is administered by the Department of Biodiversity, Conservation and Attractions and approved by the Minister for Environment after considering advice from the Gorgon Barrow Island Net Conservation Benefits Advisory Board. We also wish to thank the many collectors who contributed specimens to this study, without whom this study would have been impossible.

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Immature stages of the butterfly *Erina gilesi* (M.R. Williams & Bollam, 2001) (Lepidoptera: Lycaenidae): description and comparative morphology of *Erina* species

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ABSTRACT – The lycaenid butterfly *Erina gilesi* (Williams & Bollam, 2001) is endemic to south-western Western Australia where it is a host specialist of the vine *Cassytha racemosa* (Lauraceae). We describe, illustrate and compare the immature stages of *E. gilesi* from two sites south of Perth with other members of the genus. We also illustrate and document variation in larval colour pattern in *E. erina* (Fabricius, 1775) and *E. delospila* (Waterhouse, 1903) for the first time. The immature stages of *E. gilesi* are most similar to its sister species, *E. hyacinthina* (Semper, 1879), but the late instar larvae differ in having a pair of conspicuous white dorsolateral lines on the body, and the reddish dorsal patches on abdominal segments 1 and 6, which when present, are simple and not raised into projections. The biology of *E. gilesi* indicates that adults are seasonal and partially bivoltine, with a facultative pupal diapause. A review of larval food plant-butterfly associations indicates that each species of *Erina* Swainson, 1833 tend to specialise on different species of *Cassytha*, and generally only one or two plant species are utilised throughout the geographical range of each species/subspecies, suggesting ecological differentiation in the genus.

KEYWORDS: Candalidini, *Cassytha*, Lauraceae, life history, pupal diapause, Western Australia

INTRODUCTION

The butterfly genus *Erina* Swainson, 1833 contains six species, most of which are endemic to Australia (Braby et al. 2020). They occur in a variety of temperate and tropical woodlands and heathy woodlands where the larvae feed exclusively on *Cassytha* (Lauraceae) (Table 1). The Western Dusky-blue, *Erina gilesi* (Williams & Bollam, 2001), is endemic to the south-western Australian biodiversity hotspot, defined by Hopper and Gioia (2004), where it has been recorded from a limited area along the west and south-west coast between the Porongurups and Stirling Ranges, West Cape Howe and near Perth, Western Australia (Edwards and Kerr 1978; Williams et al. 1993; Williams et al. 1997; Braby 2000; Williams and Bollam 2001; Williams and Williams 2006; Williams et al. 2012). Recorded localities include Yalgorup National Park, Lake Preston, Myalup, Dunsborough, Yallingup, Margaret River, Augusta, Windy Harbour, Cosy Corner, West Cape Howe, as well as inland at Glen Forrest on the Darling Range east of Perth, south to Manjedal Brook, Hoffmans Mill, Manjimup, Pemberton, the Porongurups and Stirling Range National Park. It occurs in eucalypt open-forest and woodland, as well as heathland, where the larval food plant *Cassytha racemosa* Nees commonly grows as a twining hemiparasite (Williams and Bollam 2001). The taxon was originally described by Williams and Bollam (2001) as a subspecies of *Erina hyacinthina* (Semper, 1879), but Williams and Williams (2006) suggested its status may warrant investigation after both *E. gilesi* and *E. hyacinthina* were found together on Mondurup Peak, Stirling Range, with no evidence of hybridisation. Subsequently, Braby et al. (2020) proposed that *E. gilesi* be treated as a distinct species based on fundamental differences in genitalic

morphology and adult phenotype (15 characters), phylogenetic pattern according to molecular data and level of pairwise divergence according to mtDNA (2.8% for COI), and its narrowly sympatric distribution with *E. hyacinthina*. The immature stages of *E. gilesi*, however, have not been compared, with only the egg and early instar larvae (instars I and II) so far described (Williams and Bollam 2001). Thus, comparative morphology of the immature stages may provide additional evidence in support of the two species hypothesis proposed by Braby et al. (2020).

The aim of this paper is to describe, illustrate and compare the immature stages of *E. gilesi* with other members of the genus, particularly *E. hyacinthina*. We also illustrate and document variation in larval colour pattern in *E. erina* (Fabricius, 1775) and *E. delospila* (Waterhouse, 1903) for the first time. Life histories have been documented for all species of *Erina* except for *E. gilesi*.

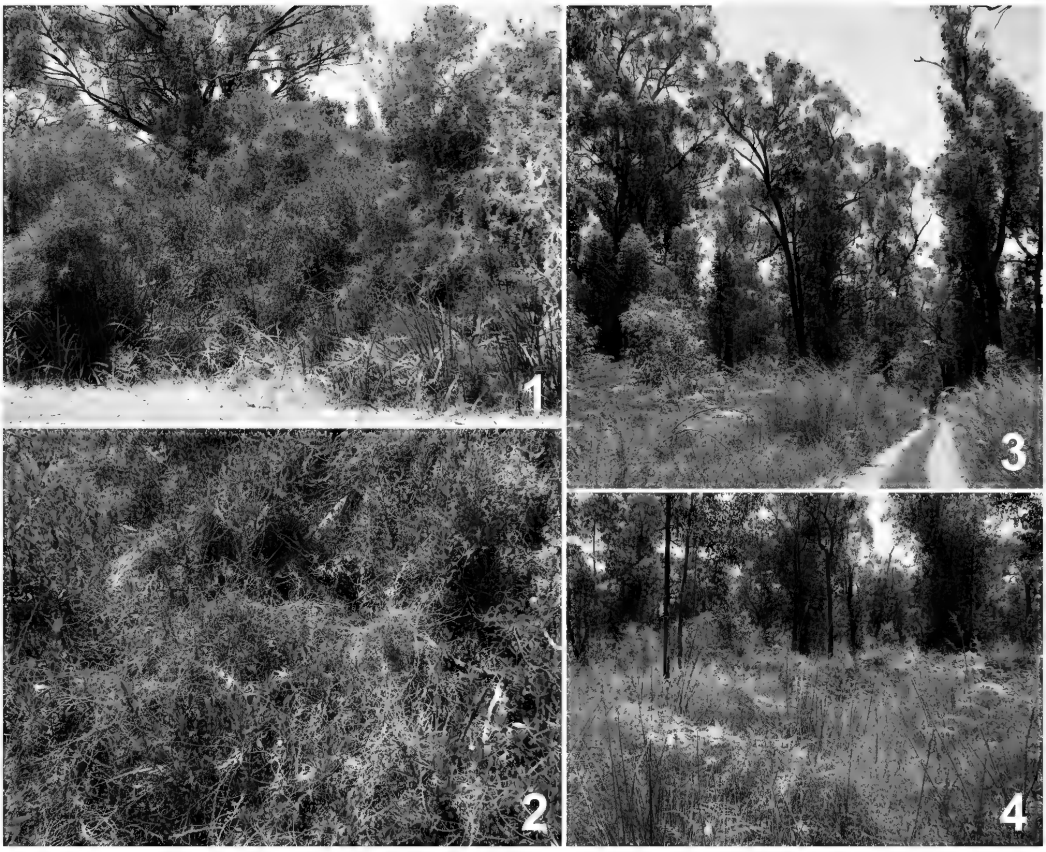
MATERIALS AND METHODS

Live material was collected from two field sites: at Lake Preston (sea-level), Myalup c. 120 km S. of Perth, Western Australia during 25 November 2019 to 16 December 2019, and Hoffmans Mill (270 m asl) on the Darling Range c. 115 km SSE. of Perth during 9 December 2019 to 11 January 2020. The habitat at Lake Preston (Figures 1–2) consists of open woodland dominated by Tuart

TABLE 1 Summary of larval food plants used by *Erina* spp. in Australia. Larval food plants are divided into two groups: primary refers to those that are used predominantly throughout the geographical range of the butterfly species or on which the immature stages are most frequently recorded where two or more food plants grow in sympatry. For the other food plants, the broad distribution is provided (at the state or territory scale), although in most circumstances these records refer to very localised associations at much smaller spatial scales.

Butterfly species	Primary food plant	Other food plants	References
Erina delospila	*Cassytha capillaris*[1, 2]		Braby (1995, 2011), Grund and Hunt (2001)
Erina acasta	*Cassytha glabella*[3]	*Cassytha pubescens* (VIC, SA), *C. peninsularis* (SA)	Fisher (1978), Grund (1996), Braby (2000), Field (2013)
Erina gilesi	*Cassytha racemosa*		Williams and Bollam (2001), this work
Erina hyacinthina hyacinthina	*Cassytha pubescens*	*Cassytha melantha* (VIC)	Braby (2000), Field (2013), Braby et al. (in press)
Erina hyacinthina simplex	*Cassytha melantha*	*Cassytha peninsularis* (SA), *C. flindersii* (SA), *C. aurea* (WA)	Fisher (1978), Grund (1997, 1998, 2001, 2009), Williams et al. (2000), Braby and Edwards (2006)
Erina geminus geminus	*Cassytha filiformis*[4]	*Cassytha pubescens* (NSW)	Edwards (1980), Braby (1995, 2011)
Erina geminus gagadju	*Cassytha filiformis*	*Cassytha capillaris* (NT)	Braby (2011, 2017)
Erina erina	*Cassytha filiformis*[5]	*Cassytha capillaris* (WA, NT), *C. aurea* (WA)	Grund (1998), Grund and Hunt (2001), Braby (1997, 2000, 2011)

[1] The record of *Cassytha filiformis* for *Erina delospila* from the Burra Range, Qld (Braby 1995) is erroneous and refers to *C. capillaris* (see Braby 2011).
[2] The record of *Cassytha glabella* for *Erina delospila* from Broome, WA (Braby 1995) is erroneous and most likely refers to *C. capillaris*.
[3] The record of *Cassytha filiformis* for *Erina acasta* from Port Denison, WA (Grund 1998) is erroneous and most likely refers to *C. glabella*.
[4] The record of *Cassytha pubescens* for *Erina geminus geminus* from the Burra Range, Qld (Braby 1995) is erroneous and refers to *C. filiformis* (see Braby 2011).
[5] The records of *Cassytha pubescens* for *Erina erina* from several locations in northern Queensland (Braby 1997) are erroneous and refer to *C. filiformis* (see Braby 2011).



FIGURES 1–4 Habitats and larval food plant of *Erina gilesi* in south-western Western Australia: 1) open woodland dominated by Tuart (*Ecalyptus gomphocephala*) and Peppermint (*Agonis flexuosa*) with small *Melaleuca* trees cloaked in *Cassytha racemosa* in lake-fringing vegetation at Lake Preston, Myalup; 2) larval food plant, *Cassytha racemosa*, Lake Preston; 3–4) riverine woodland dominated by Yarri (*Eucalyptus patens*) with a mixed understorey of *Agonis* sp., *Astartea*, *Mirbelia dilatata*, *Gahnia* sp. and *Pteridium esculentum* along a watercourse at Hoffmans Mill. Note the Hoffmans Mill site was extensively burnt by wildfire in January 2016. (Images R. Eastwood.)

(*Eucalyptus gomphocephala*) and Peppermint (*Agonis flexuosa*), with small *Melaleuca* trees and a mixed understorey of *Lepidosperma gladiatum*, *Gahnia* sp., *Acacia* spp., *Alyxia buxifolia*, *Spyridium globulosum* and *Persoonia longifolia*. The larval food plant, the vine *Cassytha racemosa*, grows patchily along the western fringe of the lake where it cloaks the *Melaleuca* trees and understorey shrubs. In contrast, the habitat at Hoffmans Mill (Figures 3–4) comprises riverine woodland dominated by Yarri (*Eucalyptus patens*), with a mixed understorey of *Agonis* spp., *Astartea* spp., *Mirbelia dilatata*, *Gahnia* sp. and *Pteridium esculentum* along a watercourse. *Cassytha racemosa* grows in high density in the understorey, as well as on some emergent shrubs and small trees. The site was burnt extensively in January 2016.

Females were individually placed inside clear plastic bags with cuttings of the larval food plant on which eggs were laid. Fresh tendrils and flower buds of the larval food plant were also examined and searched in the field for presence of eggs and larvae. Larvae were reared individually, initially in small plastic vials (40 mm diam. x 60 mm high) and then, in the later instars, larger plastic containers (120 mm x 80 mm x 60 mm). The containers were supplied with fresh cuttings of *Cassytha* spp., which was changed every 2–3 days – larvae reared in Perth were fed on *C. racemosa*, whereas those reared in Canberra were offered *C. pubescens*.

Voucher specimens have been lodged in the Western Australian Museum (7 ♂, 4 ♀: registration numbers WAM E105353–WAM E105363), as well as the Australian National Insect Collection, Canberra (4 ♂).

TAXONOMY

Family Lycaenidae Leach, 1815

Subfamily Theclinae Swainson, 1831

Tribe Candalidini Eliot, 1973

Genus *Erina* Swainson, 1833

Erina gilesi (M.R. Williams & Bollam, 2001)

Figures 5–22

Candalides hyacinthinus gilesi M.R. Williams & Bollam, 2001: 49–53, figures 1–4.

Candalides hyacinthinus gilesi M.R. Williams & Bollam: Braby, 2004: 261–262; Williams and Williams, 2006: 56; Orr and Kitching, 2010: 262; Braby, 2010: 14, 72; Williams et al., 2012: 60–61; Braby, 2016: 290–291.

Erina gilesi (M.R. Williams & Bollam): Braby et al., 2020: 714–716.

DIAGNOSIS

The immature stages of *Erina gilesi* (Figures 5–22) are similar to those of *E. hyacinthina* (Figures 23–37), but they diverge in the late instar larvae (instars III–V). In *E. gilesi*, the larva has two conspicuous white longitudinal lines, whereas in *E. hyacinthina* these lines are usually absent or, if present, yellow and only faintly visible. In *E. gilesi*, the two small dark reddish dorsal patches or spots on abdominal segments 1 and 6, when present, are not raised from the surface, whereas in *E. hyacinthina* these patches appear as projections, are larger and more variable in extent (sometimes being present only on A1 and absent on A6), and are sometimes bordered laterally by white and dark red dorsolateral streaks. Overall, the larva of *E. gilesi*, like *E. acasta* (Cox, 1873), is less variable in colour pattern; in *E. hyacinthina* the larva is usually devoid of conspicuous longitudinal markings or has a faint yellow dorsolateral line, but occasionally there may be a broken white dorsolateral line edged below by a broken dark reddish line, from the metathorax to abdominal segment 6. In *E. acasta*, which occurs parapatrically with *E. gilesi*, the larva (Figures 38–40) has a pair of conspicuous yellow longitudinal lines, rather than the white lines in *E. gilesi*.

DESCRIPTION

Egg

0.6 mm diameter by 0.4 mm high (n = 22); pale green when laid, later changing to white; subspherical, with micropylar region slightly depressed, coarse reticulate pattern of facets comprising deep quadrangular- or pentagonal-shaped polygons separated by raised ridges (Figure 5).

First instar larva

1.2 mm long; head pale brown, hidden beneath prothorax; prothoracic plate grey with several colourless setae; mesothorax yellowish-brown with two pairs of long, recurved dorsolateral setae, one on either side; metathorax and abdominal segments 1–7 yellowish-brown, each segment bearing a pair of long, recurved brown dorsal setae, laterally fringed with one long and two shorter colourless setae, and a few minute brown dots; abdominal segments 7 and 8 each with a long, recurved brown lateral seta; anal plate grey with several colourless setae (Figure 6).

Second instar larva

3.9 mm long; prothoracic plate pale green, diamond-shaped; mesothorax, metathorax and abdominal segments 1–6 pale lime-green with a broad whitish dorsal band enclosing a narrow reddish middorsal line and obscure red subdorsal markings, particularly on A1 and A6, each segment with two pairs of long, recurved brown dorsal setae and laterally fringed with colourless setae; abdominal segments 6–8 lime-green with obscure red lateral markings; anal plate reddish; entire body with a narrow white lateral line and covered with minute brown dots (Figures 7–8).

Third instar larva

8.0 mm long; similar to instar IV, but dorsal area between the pair of white dorsolateral lines paler, almost forming a broad whitish dorsal band from mesothorax to abdominal segment 6; a narrow white lateral line along length of body (Figures 9, 10).

Fourth instar larva

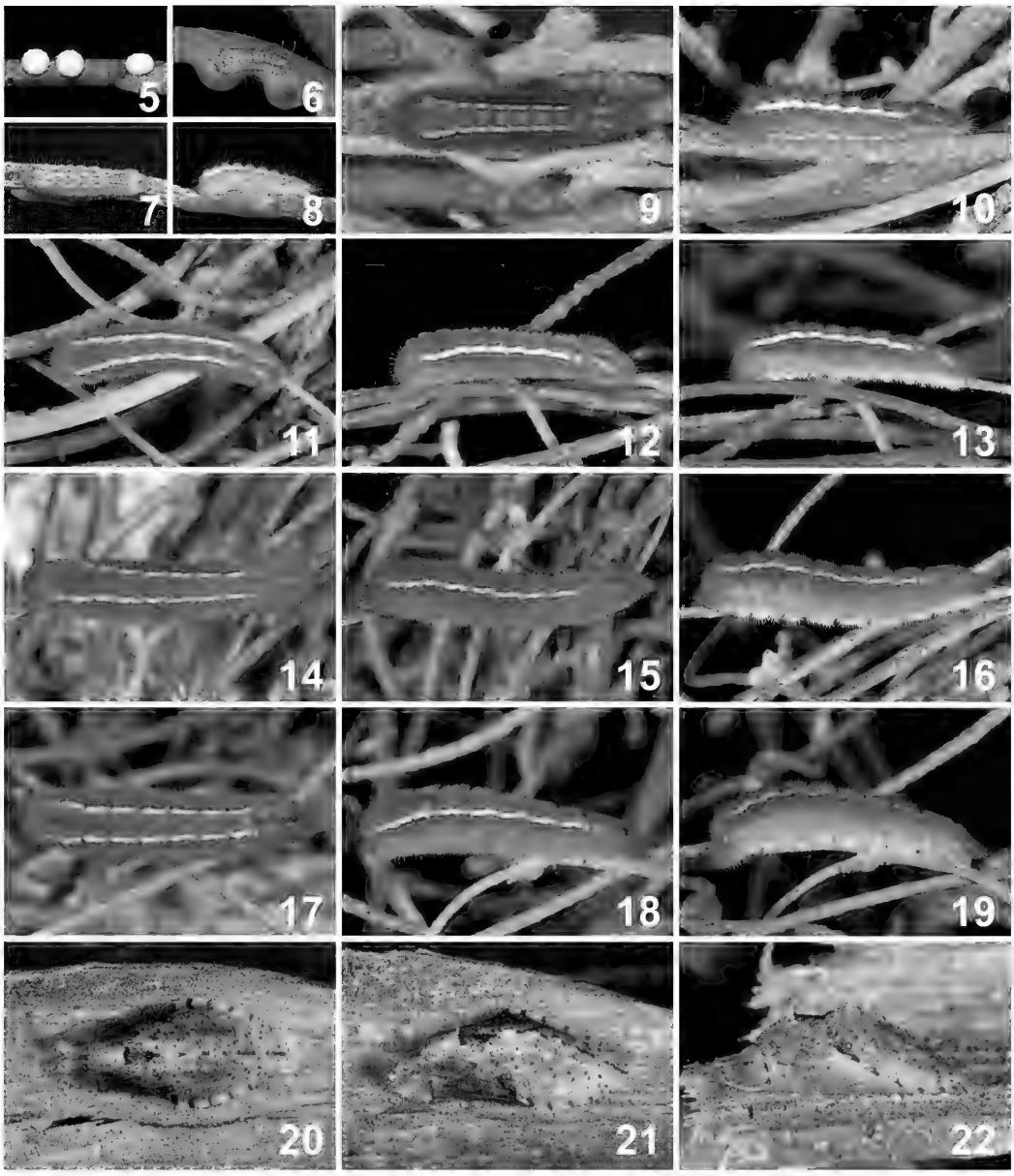
12 mm long; similar to instar V (Figures 11–13).

Fifth instar larva

15 mm long; head pale brown, concealed beneath prothorax; prothorax green, unmarked; mesothorax, metathorax and abdominal segments 1–6 green, each with a narrow darker green middorsal line, a faint pale green subdorsal streak, followed by a conspicuous white dorsolateral line edged below darker green; abdominal segments 7–10 green, somewhat flattened with a darker green middorsal line, obscure pale green subdorsal streaks on A7–A9, Newcomber's Organ present on A7, a pair of tentacular organs on A8, and a darker green anal plate on A10; body covered in dense short marginal hairs and minute dark brown secondary setae; spiracles pale brown (Figures 14–19).

Pupa

10.1–12.3 mm long ($\bar{x}$ = 11.1 mm) by 4.6–5.6 mm wide ($\bar{x}$ = 5.0 mm) (n = 31); grey-brown or brown with darker brown-black markings; head with anterior end flattened into a flange with a prominent median indentation; thorax with a pair of short slender middorsal projections; metathorax with a black dorsal ridge; abdomen with a dorsal ridge, more prominent on segments 1–3, and a conspicuous lateral flange, weakly upturned; spiracles cream (Figures 20–22).



FIGURES 5–22 Immature stages of *Erina gilesi*: 5) egg; 6) first instar larva, dorsal view; 7–8) second instar larva, dorsal and lateral views; 9–10) third instar larva, dorsal and lateral views; 11–13) fourth instar larva, dorsal, dorsolateral and lateral views; 14–16) fifth instar larva, dorsal, dorsolateral and lateral views; 17–19) fifth instar larva, dorsal, dorsolateral and lateral views; 20–22) pupa, dorsal, dorsolateral and lateral views. (Images 5–8 courtesy Jean Hort; 9–22 M.F. Braby).

VARIATION

The larvae (instars III–V) sometimes have two reddish dorsal patches, on abdominal segments 1 and 6, and occasionally an additional reddish dorsal patch on abdominal segment 8 (Figures 17–19). Most late instar larvae are uniformly green, but one final instar larva collected from Hoffmans Mill was yellow-green with distinct reddish spots on A1 and A6. Pupal colour varied according to the colour of the substrate on which the larva pupated.

BIOLOGY

The following field observations were made at the two sites south of Perth. Males were observed to either patrol across and around the understorey vegetation on which the *Cassytha* food plant was attached, or perch on prominent leaves of emergent vegetation where fresh green shoots of *Cassytha* were growing within c. 300 mm. Males actively defended their territories from other males and returned to their perching sites after each male-male interaction to wait for females. They were most active on sunny days from 08:00–15:00, with an apparent peak in abundance just after midday (13:00), when maximum temperatures were < 30°C. However, they changed their perching sites and territories according to the position of the sun, avoiding shadows during the day. Freshly emerged females flew close to the understorey and along natural pathways in the breeding sites where they encountered males and mated immediately. Once mated, some females laid an egg or two at or near the mating site before flying off to spend most of their time in the understorey.

Eggs were usually laid singly, but occasionally in loose groups of two or three, on bracts, flower buds, new soft tendrils, stems and occasionally haustoria of the larval food plant growing in sheltered positions in the understorey. Eggs laid on flower buds were difficult to detect because their colour, size and shape closely matched the small new buds. On hatching, the first instar larvae chewed a small hole at the top of the egg through which they escaped, but they did not consume the remainder of the egg shell. The first instar larvae were uniformly straw coloured on hatching, but became more speckled as they grew before moulting to the second instar. First and second instar larvae fed by chewing a shallow pit into a fresh stem or tendril towards the tip of the vine. Presumably, they also imbibed the phloem that seeped into the pit. Later instar larvae consumed the entire tendril as they moved backwards along the stem. They also ate the flower buds. When reared in captivity, final instar larvae left the food plant and pupated beneath pieces of bark or on dead leaves, which suggests they pupate in the leaf litter in nature. The pupae were attached to a silken pad, spun on the substrate, by the anal hooks of abdominal segment 10 and a silken girdle spun over the junction between the metathorax and abdominal segment 1. Pupae were heard to stridulate; however, those that entered diapause did not stridulate.

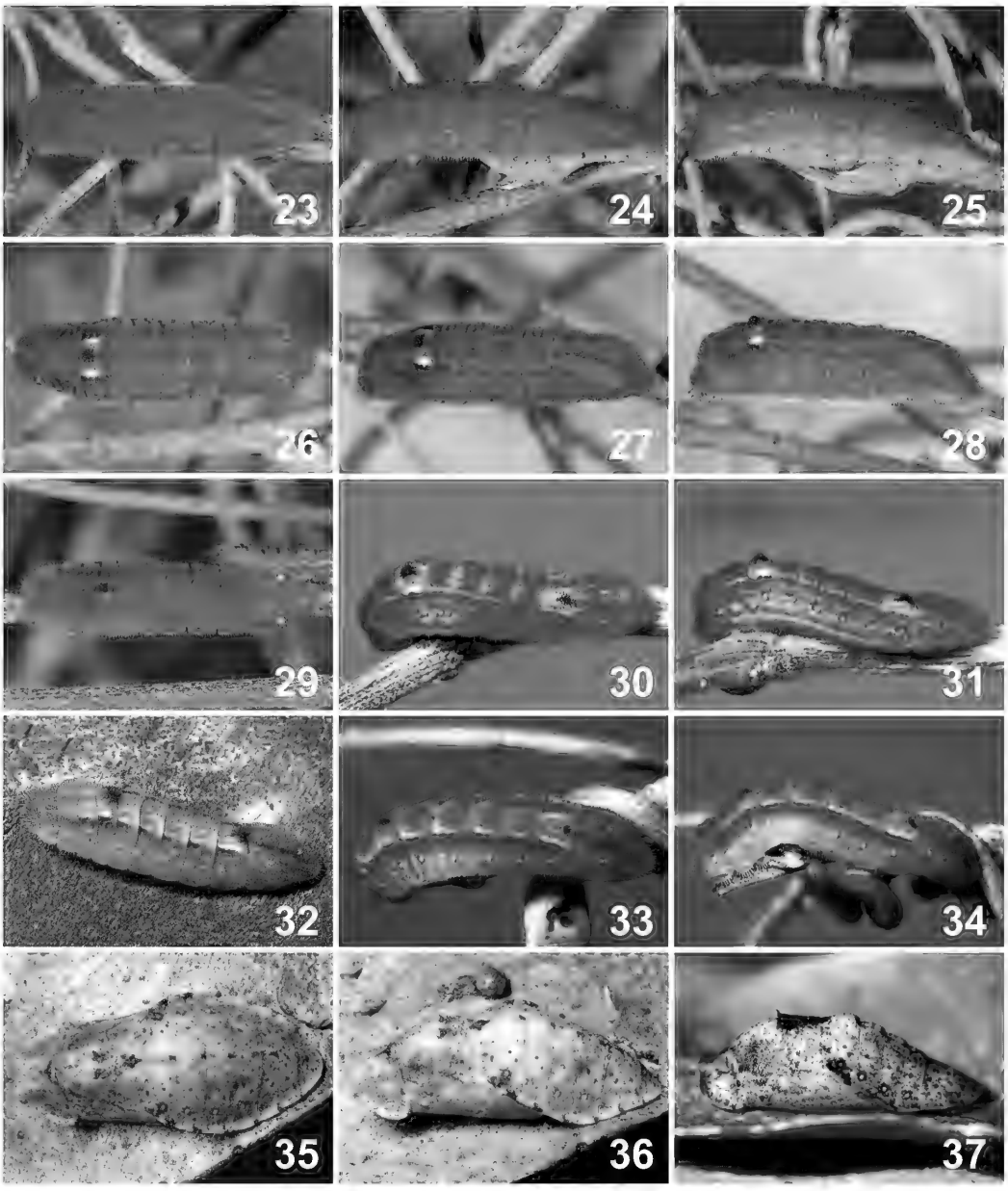
Eggs laid by captive females hatched approximately one week later (range 6–8 days, $\bar{x}$ = 7.0; n = 26). Larvae completed development in 15–20 days ($\bar{x}$ = 17.2; n = 26), with the pre-pupal stage lasting 2–3 days. Pupal duration varied: from a sample of 31 pupae, 16 (52%) emerged directly within 12–18 days ($\bar{x}$ = 14.4), whereas the remaining 15 (48%) entered diapause.

DISCUSSION

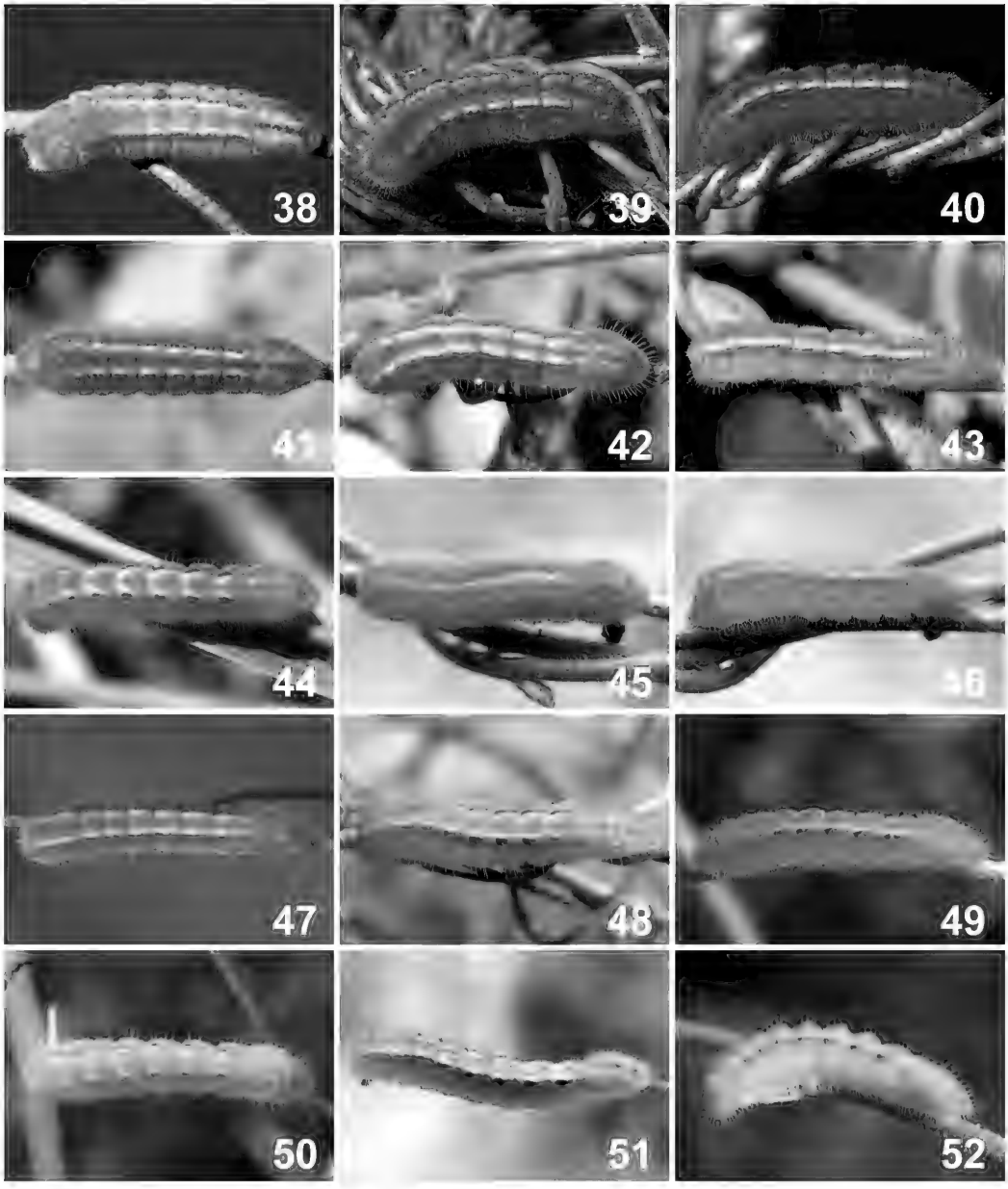
Erina gilesi belongs to a monophyletic group that includes five other species of *Erina*. According to a recent molecular phylogeny of the Candalidini, phylogenetic relationships of the six species of *Erina* are as follows: *delospila* + (*acasta* + ((*gilesi* + *hyacinthina*) + (*geminus* + *erina*))) (Braby et al. 2020). Thus, *E. gilesi* is most closely related to *E. hyacinthina*, and this pair is sister to *E. geminus* (E.D. Edwards & Kerr, 1978) and *E. erina*. Comparative differences between the immature stages of *E. gilesi* (Figures 5–22) and *E. hyacinthina* (Figures 23–37) support the species level status of the taxon recently proposed by Braby et al. (2020). Although the egg, first instar larva and pupa are indistinguishable between the two species, they diverge in the late instar larvae, with at least two character states unique to *E. gilesi*: (1) body with dorsolateral line white and conspicuous; and (2) abdominal segments 1 and 6 each with reddish dorsal patches, when present, simple and not raised into projections.

The larvae of *E. geminus* (Braby 2017, figures 21–29), *E. erina* (Figures 41–52) and *E. delospila* (Figures 53–67) from northern Australia are particularly variable, and perhaps more so than *E. hyacinthina*. Although all three species are allopatric with *E. gilesi*, larval identification can potentially be confusing. Braby (2011) noted that the larvae of *E. erina* and *E. delospila* were polymorphic, varying from green, through pale green-brown, pale brown to pinkish-brown, and in the colour of the longitudinal (dorsal) lines and bands, but these forms or morphs have not previously been illustrated. In one form of *E. erina*, the dorsolateral lines are white (Figures 41–43), and thus it closely resembles *E. gilesi*. Larvae of *E. delospila*, *E. acasta* and *E. erina* lack the reddish dorsal patches or projections on abdominal segments 1 and 6, and thus these three species can usually be distinguished from *E. gilesi*, *E. hyacinthina* and *E. geminus*, which typically have these structures. Larvae of *E. delospila* are characterised by the presence of a conspicuous purple or red dorsolateral line edged above with white, whereas in *E. erina* this feature, when present, appears as a broken line or series of spots from the metathorax to abdominal segment 6 (Figures 44, 47–52).

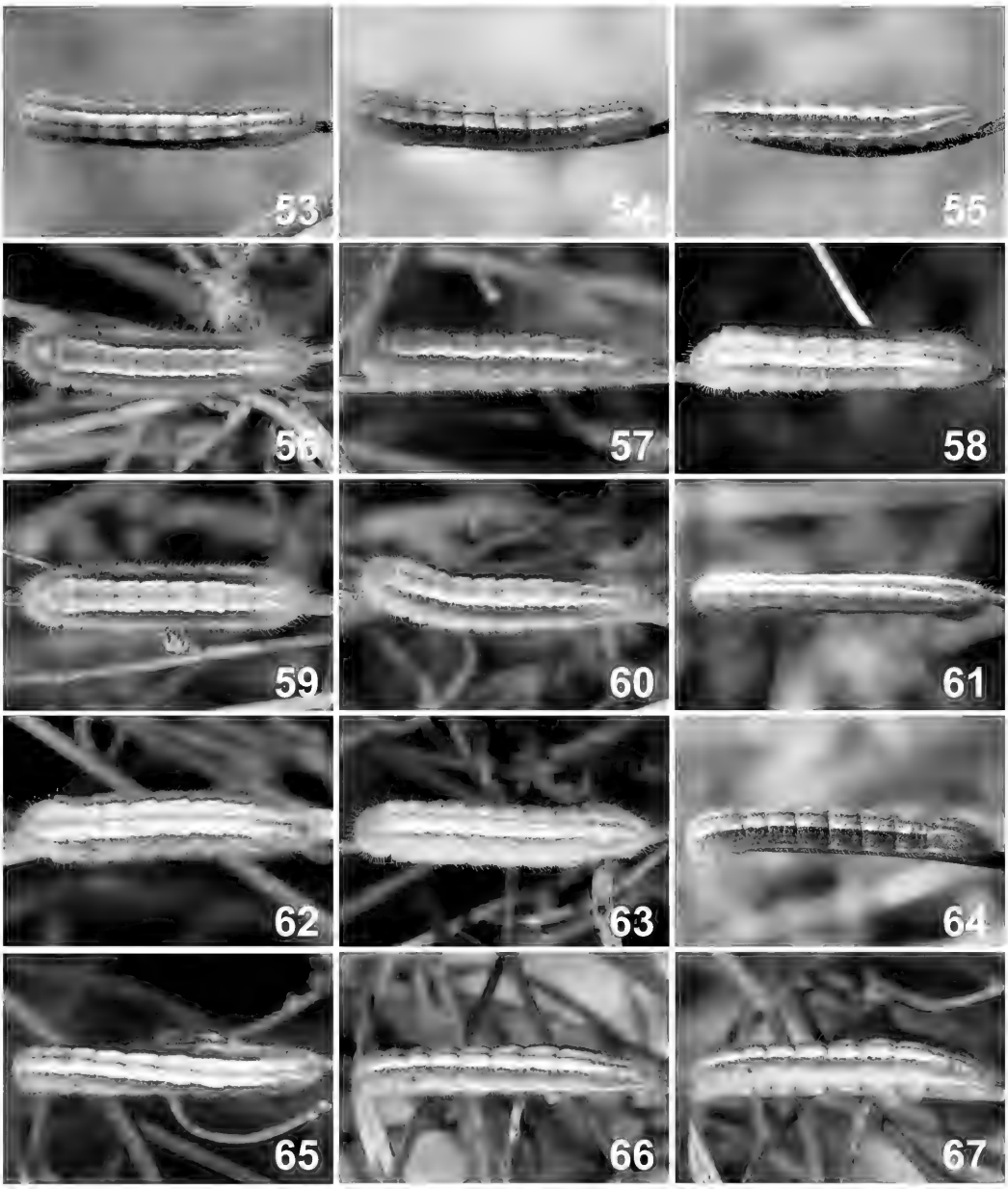
Erina gilesi larvae were not found in the company of ants in the field; however, they possess Newcomber's Organ and a pair of tentacular organs, which suggests the larvae may have a facultative association with ants, similar to other *Erina* species. Pupal stridulation also suggests the pupae may be associated with ants in their pupation sites, such as leaf litter.



FIGURES 23–37 Final instar larva and pupa of *Erina hyacinthina*, showing variation in larval colour pattern. Note tentacular organs on abdominal segment 8 are everted in Figure 29. (Images: 23–31, 33, 34, 37 M.F. Braby; 32, 35, 36 L. Hunt.)



FIGURES 38–52 Final instar larva of *Erina* spp.: 38–40) *E. acasta*; 41–52) *E. erina*, showing variation in colour pattern. Forms of *E. erina* are as follows: 41–43) 'form 1' green with white longitudinal lines; 44) 'form 2' pale green with reddish-purple longitudinal lines; 45–46) 'form 3' green with yellow longitudinal lines; 47–48) 'form 4' pale green with reddish-purple longitudinal spots and yellow dorsal band; 49) 'form 5' green with reddish-purple longitudinal spots; 50–52) 'form 6' brown with reddish-purple longitudinal spots. (Photos: 38, 41–50 M.F. Braby; 39, 40 L. Hunt.)



FIGURES 53–67 Final instar larva of *Erina delospila*, showing variation in larval colour pattern. Forms are as follows: 53–55) 'form 1' green with pale green dorsal band; 56–57) 'form 2' green with yellow dorsal band; (58) 'form 3' pale green with white dorsal band; 59–60) 'form 4' green with pink dorsal band; 61–64) 'form 5' pink-brown with pink dorsal band; 65–67) 'form 6' pink-brown with white dorsal band. (Photos: M.F. Braby.)

Erina gilesi is seasonal and appears to be partially bivoltine, with a facultative pupal diapause. Based on our larvae reared in captivity it appears that approximately half of the population of the first generation develops directly, while the other half enters diapause. Williams and Bollam (2001) recorded the broad adult flight period from October to late January, but noted that the main activity period was approximately six weeks, from late November to early January, which coincides with the flowering period of the larval food plant. At the Hoffmans Mill site, adults were still flying on 29 January 2020, and in captivity adults continued to emerge well into February.

All species of *Erina* feed on *Cassytha*, with a total of nine plant species recorded for the butterfly genus as a whole (Table 1). Several food plant determinations in the past were incorrect due to taxonomic difficulties with *Cassytha* prior to the systematic revision of the genus by Weber (2007). Available data indicate that each *Erina* species tends to specialise on different species of *Cassytha* and generally only one or two plant species are used throughout the geographical range of each butterfly taxon (species or subspecies). Only three taxa (*E. acasta*, *E. hyacinthina simplex* (Tepper, 1882) and *E. erina*) are known to exploit three or more species of *Cassytha*. An exception to this general pattern of specialisation is the species pair *E. geminus* and *E. erina*, both of which mainly exploit *C. filiformis*; however, *E. geminus* only uses this food plant where it grows on sandstone, whereas *E. erina* occurs more widely in tropical and subtropical woodland habitats outside sandstone areas. These insect-plant associations suggest a degree of ecological differentiation in the genus *Erina*.

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SHORT COMMUNICATION

Unusual discovery of the 'Australian Firebeetle' *Merimna atrata* on an older postfire area

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KEYWORDS: Australian firebeetle, forest fire, pyrophilous insects, infrared reception

INTRODUCTION

The 'Australian Firebeetle' *Merimna atrata* (Gory & Laporte, 1837) is endemic to Australia and to southern parts of Papua New Guinea (Hawkeswood 2007; Schmitz et al. 2015). As indicated by its common name, this uniform black beetle in the jewel beetle family Buprestidae is attracted to ongoing bush fires and starts to invade the freshly burnt area immediately after the active fire has gone out (Tepper 1887; Poulton 1915; Schmitz and Schmitz 2002). The reason for this pyrophilous behaviour is based on the special food source of the xylophagous larvae that can only develop in severely fire scorched trees and shrubs of the family Myrtaceae (Hawkeswood and Peterson 1982; Hawkeswood 2007; Kitchin 2009; Schmitz et al. 2015). Consequently, the adult beetles of both sexes approach fires and meet on the freshly burnt areas. The early arrival of *M. atrata* on burnt areas confers the clear advantage of smoke and heat emitted by hotspots such as burning or glowing wood and hot ashes, which keep away competitors like other wood boring insects as well as predators like birds and lizards. However, an accidental landing on a hot surface may be life threatening for a small insect. To cope with this danger, *M. atrata* has developed abdominal infrared receptors as an early warning system for hot spots (Schmitz et al. 2000; Schmitz et al. 2001; Hinz et al. 2018).

After the fire, the hot spots gradually go out and, therefore, the protective shield build by heat and smoke disappears within a few days. Hence, predators of *M. atrata*, such as the Australian Magpie (*Cracticus tibicen)* become increasingly present. Consequently, *M. atrata* disappears within three to four days after the fire and, after about five days, no more beetles can be found on the cool postfire area. This has quantitatively been documented for a small burnt area close to Yanchep National Park, Western Australia in 2014 (Schmitz et al. 2015). Furthermore, the authors have inspected more than 50 older postfire areas in the Perth Metropolitan area and in the adjacent Perth Hills in the last 15 years and have never found *M. atrata* in burnt areas more than five days old.

Thus, it was surprising that in January 2020 a noteworthy number of *M. atrata* was found in a postfire area more than one month after the fire. This unusual observation is reported here and possible reasons for the prolonged stay of the firebeetles are discussed.

MATERIALS AND METHODS

INVESTIGATION AREA

M. atrata was found in January 2020 on a burnt area created by the 'Yanchep Fire' that burnt in the beginning of December 2019. This large bushfire started on 11 December next to Wanneroo Road, about 1 km south of the intersection with Yanchep Beach Road. Within five days, the fire travelled 25 km in a north-westerly direction up to Barragoon Road south of Guilderton. In total, an area of 13,000 hectares was burnt. In Yanchep National Park, the fire burnt the forest on the western bank of Lake Loch McNess. In this area, the swampy lakeshore is covered with Swamp Paperbarks (*Melaleuca rhaphiophylla*) followed by a eucalyptus forest with River Gum (*Eucalyptus rudis*) and Tuart (*E. gomphocephala*). The small spot where we found the beetles was located inside the burnt forest on the western bank of the lake, opposite the camping and recreation area on the unburnt eastern bank of Loch Mc Ness. Where the beetles were discovered, the 'Ghost House Trail' runs very close to the lakeshore and the fire had burnt into the subterranean roots of the Swamp Paperbarks so that many trees had fallen over. From time to time small amounts of smoke emerged out of the rootholes. The investigation area bordered directly on the *Melaleuca* girdle and had a size of about 50 x 20 m (GPS coordinates 31.54404°S, 115.67713°E). Six large eucalyptus trees in the area provided preferential landing sites for the beetles (Figure 1).

COLLECTION AND DOCUMENTATION

M. atrata was observed and captured on 8 days in the period from 13–27 January 2020. Beetles were collected from the six larger trees by hand or — when resting in the ashes on the ground around the trees — by net. All captured beetles were retained and used for further morphological and neuroanatomical investigations (Collecting Permit issued by DBCA, see Acknowledgements). Thus, potential double counting was avoided.

FIGURE 1 Burnt investigation area where *M. atrata* was found: A) Southerly view showing five of the six larger eucalyptus trees used by the beetles as preferred landing sites. In the background, the lakeside with the girdle of heavily burnt swamp paperbarks is visible. Most of the paperbarks had fallen down because the fire continued to burn underground in the roots. In the lower right corner, the Ghost House Trail is visible (arrowhead) representing the western border of the area. Arrow points towards tree No. 1, about 20 m away. Inset in the lower right corner shows a *Merimna* sitting on a burnt log. B) The eucalyptus tree No. 1 that attracted most beetles. This tree was knocked over by a fallen paperbark and bordered the northern part of the observation area. Consequently, the root plate was partly lifted creating many holes (arrowheads). Smoke and hot air emitted from roots burning underground emerged from the holes.

TEMPERATURE MEASUREMENTS

Surface temperatures of the visible inner walls of the holes in ground around tree No. 1 (see Fig. 1B) were measured with a handheld infrared thermometer (Ryobi Infrared Thermometer RIT310).

RESULTS AND DISCUSSION

Over the observation period a total of 30 *M. atrata* was caught in the investigation area (Figure 1, Table 1). About a dozen additional beetles were also sighted. However, because these beetles were not captured, it cannot be ruled out that some beetles were counted twice. Occasionally a few females were observed diving with their abdomen deep into the ash, presumably in an attempt to deposit eggs under the bark of hidden roots of nearby trees. Copulation attempts by males were also seen. Most beetles were seen and caught on Tree No. 1 or close to this tree on the ash covered ground (Figure 1B). On one day, six beetles could be observed simultaneously on this tree for some minutes.

To confirm that the beetles occurred only on the observation site, inspection rounds in the burnt eucalyptus forest adjacent to the investigation area were made 2–3 times on each observation day. Rounds were made parallel to the investigation area about 30–40 m to the west of the 'Ghost House Trail', which represented the western boundary of the investigation area. During these 20 rounds only four beetles were observed. These beetles were rather furtive and flew away when the observer approached. Farther away from the investigation area (e.g. when approaching the observation site from the Yanchep Beach Road) we never saw any beetles in the burnt forest. In contrast, the beetles in the investigation area were more or less stationary. Males flew from tree to tree in search for females, and a few females deposited their eggs. In principle, beetles showed the same behaviour as observable on freshly burnt areas (Schmitz et al. 2015), though with a reduced intensity. As a result, the prolonged presence of *M. atrata* on the inspected area more than a month after the fire was rather unusual.

TABLE 1 Beetles captured on the survey area.

Date	No. of beetles captured	Observation Period
13 January 2020	2	10:30–14:00
15 January 2020	3	10:00–14:00
16 January 2020	7	10:15–14:15
18 January 2020	4	10:00–14:15
19 January 2020	2	10:00 –14:00
25 January 2020	8	11:00 –14:30
26 January 2020	3	10:30–14:00
27 January 2020	1	10:30–14:15

There are several possible explanations for why *M. atrata* persisted at this site so long after the fires had passed. First, the 'Yanchep Fire' burnt for five days with a high intensity and is likely to have attracted a large number of beetles. These beetles found favourable conditions in the freshly burnt area and, therefore, stayed as long as burning or smouldering *Eucalyptus* wood was present. With high sensitivity, *M. atrata* can smell odours characteristic of burning gum wood, such as eucalyptol, and also some other volatile organic compounds (VOCs) characteristic of burning wood more generally, such as furfural and 2-methoxyphenol (Paczkowski 2018). This acute sense of smell enables *M. atrata* to detect and select eucalyptus fires while avoiding those in banksia forests or in pine plantations (pers. obs.). Once in the freshly burnt area, the smoke profoundly alters the behaviour of the beetles, who stay in the burnt area, show nearly no escape behaviour, and engage in reproductive activities. As yet there is no evidence for sex pheromones in *M. atrata*. Therefore, it is possible that the smoke of burning gum wood has — at least partly — taken over the role of a pheromone system in attracting both sexes together for reproduction (Schmitz et al. 2015). We suggest that most probably, the small amount of smoke still emerging from underground was the reason for the prolonged stay of beetles at the site. The smoke given off by the burning roots of swamp paperbarks and flooded gums — potential breeding trees for this species — would likely have contained the right blend of odorants to attract the beetles. This scenario is especially supported by the pushed away tree No. 1. Smoke escaped permanently out of the openings around the lifted root plate. Although the smoke was mostly hard to see, temperature measurements of the inner walls of the openings around the tree always yielded temperatures of about 100° C, indicating a constant flow of gases from combustion emitted by the smouldering roots. This tree was clearly favoured by the beetles.

In summary, the special conditions in and around the investigation area made this spot into a small 'habitat island' of favourable conditions for the Australian firebeetle long after the fire. This likely continued to attract new beetles from the closer surroundings that became aware of the smell of burning for as long as the site continued to smoke.

ACKNOWLEDGEMENTS

We are indebted to the Department of Biodiversity, Conservation and Attractions (DBCA) in WA for issuing the Fauna Taking Licences No. FO25000232 from 06/01/2020. Brian Inglis, Clayton Sanders and Leigh Sage from the Parks and Wildlife Service of DBCA in Wanneroo permitted access to the burnt areas and supported our fieldwork. We thank two anonymous referees for their helpful comments.

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Nesting biology of the Australian solitary bee *Paracolletes crassipes* Smith (Hymenoptera: Colletidae) accords with that of the Diphaglossinae

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ABSTRACT – Discovery of an extensive nesting aggregation of *Paracolletes crassipes* in south-western Western Australia enabled the first study of the nesting biology of this species and its genus. Nest burrows were excavated in deep loam in a clearing in sclerophyll forest. Like New World Diphaglossinae, females of *P. crassipes* constructed vertically oriented brood cells with strongly curved, polished necks; larval provisions were partly liquid and partly solid; mature larvae spun cocoons with flat tops and produced a clear liquid (evidently from the Malpighian tubules) at the time of defaecation. The cocoons of *P. crassipes* differed from those of other diphaglossines in having solid tops and no covering of the larval faecal masses. Overall, the nesting biology tends to support the inclusion of *Paracolletes* in the Diphaglossinae.

KEYWORDS: brood cells, cocoons, floral preferences, larval provision, mate-seeking

INTRODUCTION

Paracolletes crassipes Smith is a medium-sized, black, hairy bee that is recorded from both eastern and western Australia (Atlas of Living Australia, accessed March 2020). Western Australian Museum collection records reveal that, in Western Australia, the species occurs south of a line from Jurien to Israelite Bay. Despite its widespread occurrence, its nests and nesting biology have not been documented previously.

In early 2020, the serendipitous discovery of a large nesting aggregation near Waroona in south-western Australia provided an opportunity to glean details of the nesting biology of this species, indeed the genus *Paracolletes s. str.*, for the first time. The present paper summarises the results of studies at the nesting site and in the laboratory and should be of interest to bee systematists and ethologists alike.

Paracolletes crassipes has special significance in being the type-species of the genus *Paracolletes* Smith, 1853, which is the type-genus of the tribe Paracolletini Cockerell, 1934 (Michener 1986a). Until comparatively recently, this tribe formed part of the subfamily Colletinae and contained all of Australia's hairy, scopa-bearing colletids and most of those of South America (Michener 1944, 1965, 2007). Unexpectedly, genetic studies (Almeida and Danforth 2009) indicated that *P. crassipes* is more closely related to members of the New World Diphaglossinae than to other hairy colletids, even including *Anthoglossa* Smith which Michener (1965, 2007) had treated as a subgenus of *Paracolletes*. Accordingly, Almeida et al. (2012) removed *Paracolletes* from the clade containing the bulk of the bees previously known as Paracolletini and adopted the subfamily name Neopasiphaeinae (proposed originally as a tribe by Cockerell, 1934) for this assemblage. *Paracolletes* remained *incertae sedis* until being included in Diphaglossinae by Almeida et al. (2018).

Because members of the Diphaglossinae exhibit some very distinctive features of nesting biology that sets them apart from other hairy colletids (Rozen 1984; Almeida 2008), details of the nesting biology of *Paracolletes s. str.* have been keenly awaited.

METHODS AND MATERIALS

My observations of nests and nesting and mating behaviour were made on Cypress Farm, c. 10 km ENE of Waroona and c. 94 km S. of Perth CBD, Western Australia. I excavated nests and observed adult activity on three occasions in early 2020: 24 January, 29–31 January, and 5–7 March. On 24 January, I began digging where male activity was most intense and females were sighted entering or leaving burrows. Excavation was undertaken using hand tools and the spoil was

put through a 5 mm sieve to extract brood cells and live stages. The resultant pit, which reached a depth of 80 cm, was then covered with a sheet of tin until I resumed excavation on 29 and 30 January, extending it on one side. The pit was back-filled on 31 January and a second, smaller excavation was commenced several metres away to trace an open burrow into which a pollen-laden female had been seen entering. During my March visit, I reopened the larger pit, deepening it to 102 cm and extending it into undisturbed soil on two sides.

Cells containing live stages were refrigerated until they could be returned to the laboratory where they were kept in an insulated box maintained indoors at ambient temperatures. Voucher specimens are lodged in the entomology collection of the Western Australian Museum, Perth.

Bombyliid flies collected at the nesting site were identified with the assistance of David Yeates (Australian National Insect Collection) and keyed using the work of Li and Yeates (2019). Meloid beetles were keyed to genus using the work of Bologna et al. (2013).

Cocoon tops were examined and imaged using a Hitachi TM3030Plus electron microscope.

RESULTS

NESTING SITE

On 24 January, I discovered an extensive nesting aggregation of *P. crassipes* in a forest clearing known as 'Donkey Paddock' on Cypress Farm (Figure 1). The clearing was created as the shunting yard for timber loading in the late 1800s or early 1900s in a valley floor adjacent to Cypress Brook. The ground was mostly gently sloping with some level areas, the soil a red-brown loam. Initially, I did not see the nests, but a persistent hum drew my attention to males of *P. crassipes* hovering close to the ground at the edge of a vehicle track. There, the ground was covered by dense, very short grass, moss and leaf-litter. Occasionally, males converged on and attempted to copulate with a crawling female and, now and then, a pollen-laden female flew in and disappeared among the grass and litter. Thus, the presence of numerous concealed burrows was revealed. This adult activity extended for approximately 90 m in a 2–4 m wide band flanking the track. On later visits, similar adult activity revealed more nest burrows in adjacent areas of the clearing, some being in open bare ground.

Surrounding the clearing was almost pristine sclerophyll forest dominated by Jarrah (*Eucalyptus marginata* Smith), Marri (*Corymbia calophylla* (Lindley)) and Swan River Blackbutt (*Eucalyptus patens* Bentham). During my two January visits, *C. calophylla* was in heavy flower, but, on my March visit, few flowers remained. No other native plants were observed to be in flower in the area at the same times.

FIGURE 1 Forest clearing where an extensive nesting population of *Paracolletes crassipes* was studied. Many nest burrows were located just to the right of the track among the leaf litter.

ADULT ACTIVITY AT NESTING SITE

During my two January visits, males were extremely numerous over the nesting site where they flew in meandering paths one or two centimetres above the grass and litter or the bare ground surface. They frequently landed to investigate holes and, occasionally, they converged upon a female crawling on the ground or litter and attempted to copulate with her. During my March visit, by contrast, no males were observed.

On my first visit to the site (24 January), the day was clear, sunny and very warm. From about 11 am, when my observations commenced, male mate-seeking activity was confined to ground shaded by tall trees. However, as that area became exposed to full sunlight in the early afternoon, it was progressively deserted by the males. On 29 January, under similar conditions, males again patrolled the nesting area until it was exposed to the sun, but, from 2.30 pm, males patrolled shaded ground on the opposite side of the clearing. After 4.30 pm, males patrolled both sides of the clearing and continued to do so until 7.30 pm when light was fading. On 30 January, cooler, cloudy conditions prevailed following overnight showers and males patrolled the full width of the clearing from 9 am onwards. Even after the cloud broke about 4.30 pm, male activity continued over areas receiving full sun.

Females were active on all three of my visits. In January, I observed many fewer females than males and most were sighted returning to burrows, their hind legs laden with whitish pollen. Others were seen hovering over the ground, occasionally landing and scratching at the soil or investigating holes. During my March visit, all females returning to burrows lacked pollen loads and the wing margins of all collected specimens were heavily nicked or tattered. On all days of observation, the numbers of females returning to burrows increased towards evening, the latest arrivals being noted at 7.30 pm when fading light made it difficult to see them.

NESTS

Nest entrances, identified by the movement of females in or out, were mostly hidden among grass and leaf litter, but a few were in open bare ground. Some entrances had a small lateral tumulus while others had none. Burrows were difficult to trace because of grass and tree roots or stones, but entered obliquely, c. 20–25° below horizontal for 10 cm or more, then gradually became steeper, their walls being unlined. One burrow was followed for 47 cm, at which point its slope was c. 45°.

Many more old, vacated cells and cocoons were excavated than cells containing live stages. They were recovered from depths of 24 cm to 85 cm. Cells containing live stages were recovered from depths of 30–78 cm. Whether old or new, cells occurred singly, not in clusters. Careful excavation of cells in situ revealed that their long axes were vertical, and they were situated at the ends of rising lateral burrows (Figure 2). Unfortunately, lateral burrows could not be traced to their connections with shafts, so their lengths remain unknown. However, the lateral shown in Figure 2 measured at least 39 mm.

Several cells that appeared to be freshly constructed but lacked provisions had smooth, shining inner walls including the curved 'necks' (Figure 2). When a lump of loam containing half of one such cell was soaked in water, most soil slumped away, but a layer approximately 1 mm thick surrounding the cavity remained intact, suggesting the soil had been cemented by some secretion. At the broken edges of this cell piece, it was evident that a very delicate membrane of cellophane-like material (CLM) lined the cell cavity and was responsible for the shine, but it was not easily peeled away from the soil.

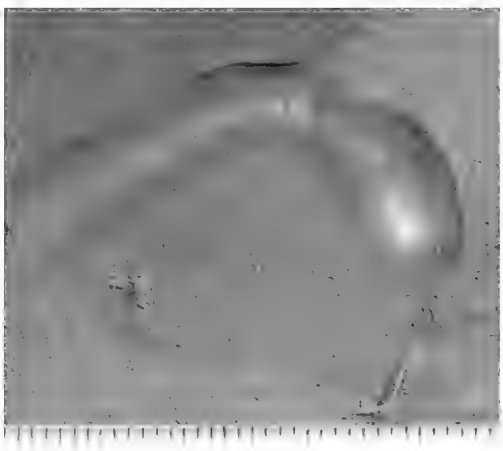


FIGURE 2 *Paracolletes crassipes.* Incomplete cell and lateral burrow showing how shining, secreted lining of cell walls continues into curved neck. The cellophane-like cell capsule had not yet been constructed. Scale in mm.

The walls of all cells containing provisions or a cocoon had a second lining of CLM that extended up to (but not into) the curved neck and extended just a few millimetres beyond the cocoon top. This membrane, though very delicate, could be peeled away from the walls and the cocoons.

Lateral burrows of cells containing live stages were soil-filled except for the curved cell necks. The inner end of the barricade was observed in only two cases. It was firm and smooth except for a central concavity, lacked any spiral pattern and was not plug-like. The sizes of cells varied markedly, likely corresponding to the genders of the occupants (females being larger than males in the imago). While newly constructed cells were fragile and broke during excavation, cells containing cocoons had cemented earthen coats and were easily separated from the soil as nodules.

PROVISIONS

No provisioned cells were recovered during my January visits and only three were found during my March visit. Their walls broke and became soaked with a liquid presumed to be nectar from the provision. In the base of each cell there remained a semisolid mass of whitish pollen. The pollen grains were consistent with being those of *Corymbia calophylla*.

COCOONS

Each cocoon filled the entire lumen of the cell below the neck. Despite the close application of the cocoon to the cell walls and the CLM membrane that lined them, the latter could be peeled away easily from cocoons after removal of the surrounding earthen wall.

The top of each cocoon was quite flat and formed a thick, stiff partition across the cell mouth below the curved neck of the cell and several millimetres inside the mouth of the CLM cell capsule (Figure 3). The cocoon top was tilted towards the lateral burrow so that it was not perpendicular to the longitudinal axis of the cell (Figure 4). Consequently, one can distinguish between its upper and lower portions (as distinct from its outer and inner surfaces). Its outer surface was mostly dark brown and slightly shiny, but a narrow strip around its upper rim was pale brown and matt (Figure 5).

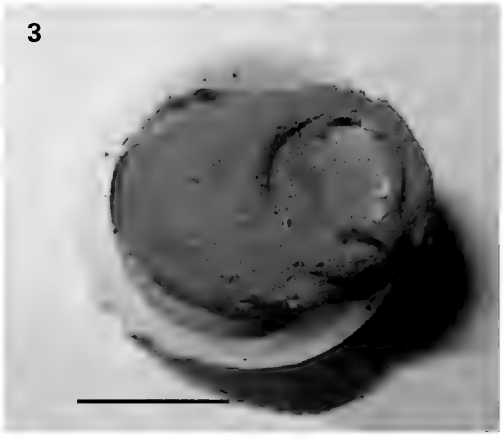
The inner surface of the cocoon top (the cocoon ceiling) was mostly flat but, around its circumference, it curved down and merged imperceptibly with the side walls. It was smooth, blackish brown and shiny except for a patch in its upper one quarter to one half which was pale brown and matt (Figure 6).

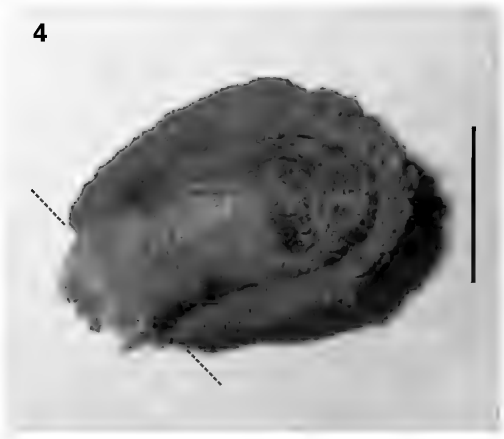
Sectioning the cocoon top revealed that it was solid and composed for the most part of five layers of silk fibres, each embedded in a polymer matrix (for convenience, I will use the term fibre-reinforced polymer, abbreviated as FRP, for such layers). Between these solid layers were very thin layers of uncemented silk strands, but no air spaces. The cocoon top was

thinnest (c. 0.3 mm) close to its lower edge and became thicker toward its upper edge (Figures 7–8). At the latter, I was able to tease apart about 20 tightly packed layers of silk fibres not embedded in a matrix (Figure 9). These uncemented layers connected the pale areas of the inner and outer surfaces of the cocoon top.

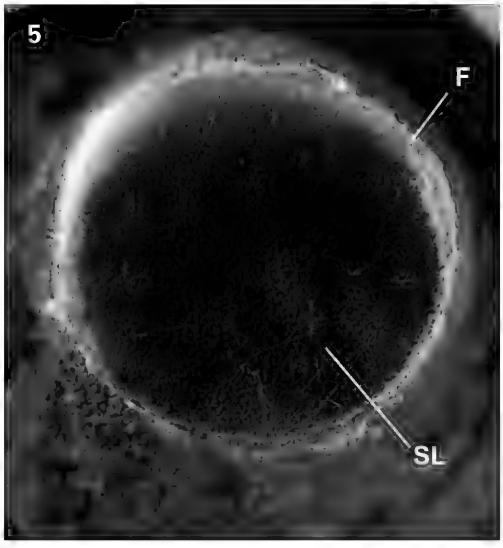
Examination with a scanning electron microscope revealed that most of the upper surface of the cocoon top lacked apertures (Figure 10). However, its pale outer edges consisted of open-weave silk fibres (Figures 11–12). The inner surface of the cocoon top was also sealed over most of its area except for a pale patch (Figure 6) which was comprised of open-weave silk fibres (Figure 13).

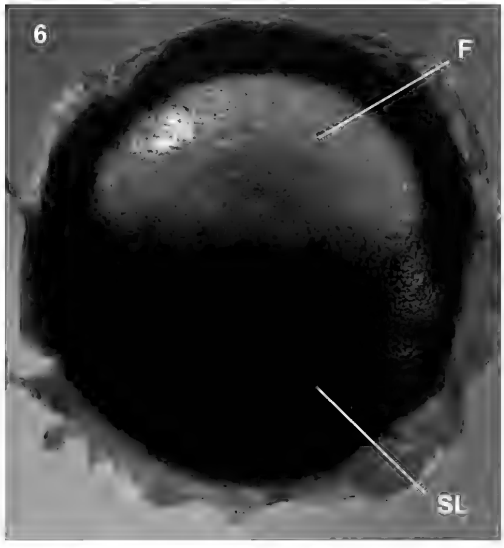
The side and bottom walls of the cocoon contrasted with the top in being composed of a thin but tough, flexible, translucent brown membrane. This membrane was double-layered 1–3 mm below the cocoon top but





FIGURES 3–4 *Paracolletes crassipes*. Earth nodule containing a cocoon: 3) top view showing cocoon top surrounded by torn edges of cell capsule; 4) lateral view (broken line indicates plane of cocoon top; whitish prepupa and blackish meconium are visible through translucent side wall of cocoon. Scales 1 cm.





FIGURES 5–6 *Paracolletes crassipes*. Cocoon top: 5), outer view; 6) inner view. F, area of open-weave silk fibres; SL, sealed lamina (silk fibres embedded in a secreted matrix).

changed imperceptibly to single-layered in the lower half. Like the sealed layers of the cocoon top, each layer of the side and bottom walls consisted of FRP and, when torn using jewellers' forceps, silk fibres were exposed along the torn edges.

Several cocoons were opened shortly after being found and most contained an inactive prepupa resting on a blackish meconium. These meconia (Figures 14–16) were moulded (more or less) to the rounded lower end of the cocoon but thick in the centre so that the upper surface of each was shallowly concave. In some cases (Figures 15–16), the contours of the undersides of meconia differed from those of the cocoon bases, suggesting air spaces had existed between the two. Individual faeces could be discerned even though they were compressed into a solid mass. No silk was laid on top of the meconium.

Clear liquid droplets were noted inside the side walls of several cocoons with prepupae and a pool of clear, watery liquid was found in one. When this liquid was transferred to a glass vial and warmed on a hotplate, it evaporated leaving a substantial deposit of whitish gummy material. Similar gummy material encrusted parts of the interior of cocoons, including the upper surface of the meconium (Figure 14). This substance, when dissolved in water, was found to contain numerous tiny, white, rounded bodies composed of densely packed spherical granules consistent with being urate crystalloids. A mature larva found in one cocoon was just beginning to defaecate. It was transferred to a glass vial where it continued to produce discrete, semi-firm, rod-like faeces and a clear colourless liquid.

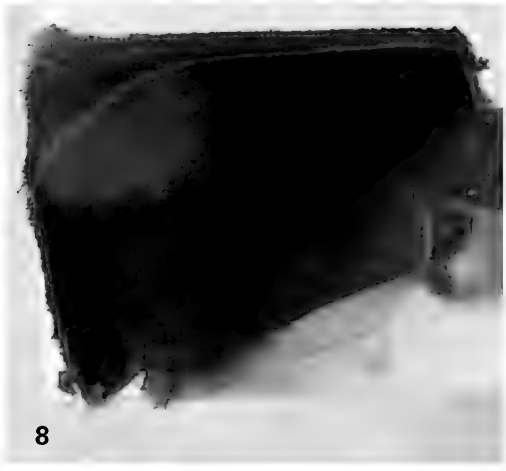
Several cells containing intact cocoons were maintained at ambient indoor temperatures. Adults of *P. crassipes* emerged from some of them: in February 2020, a male and a female; in the period 25–30 November 2020, two males and four females.

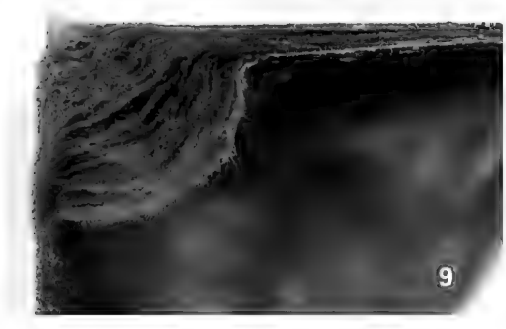
Most of the old cocoons excavated had perforated tops but several had an intact top and a hole in the side wall.

FORAGE PLANTS

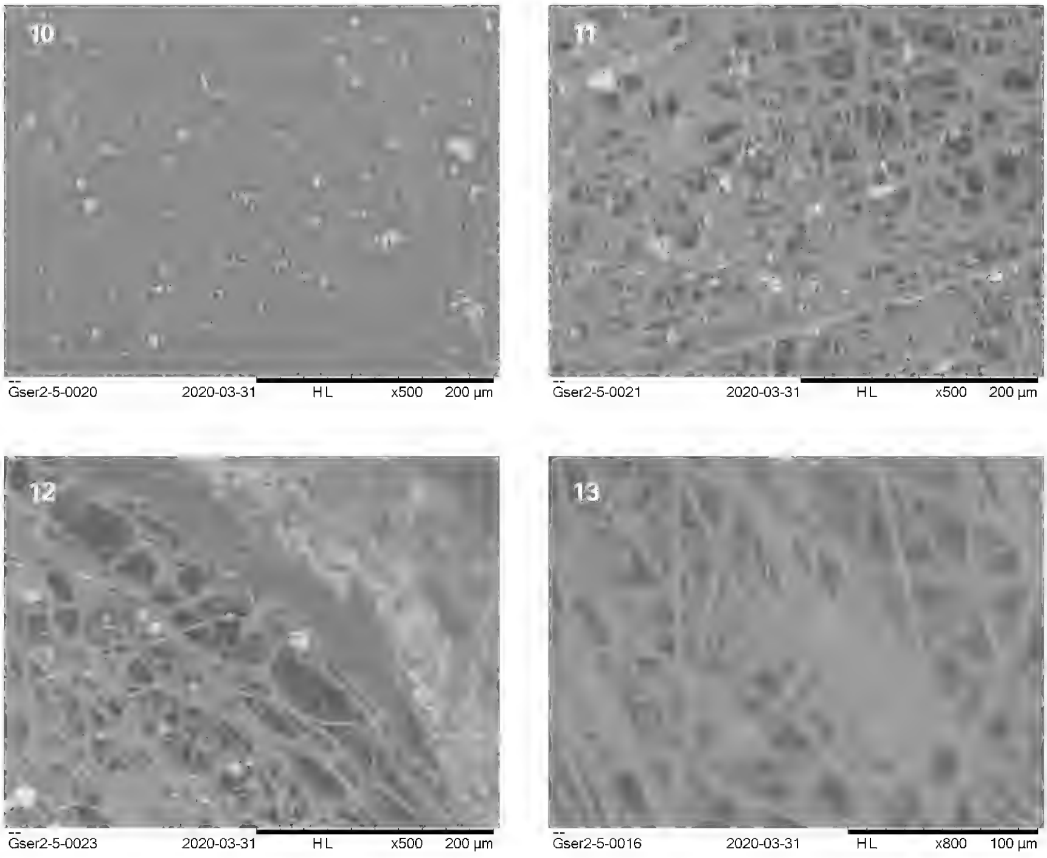
No sightings of adults at flowers were made at Cypress Farm. In January, the surrounding Marri trees (*Corymbia calophylla*) were in very heavy flower and this blossom was generally much too high to be reached with an insect net. Nevertheless, it can be assumed that this is where the bees were foraging because there were no other flowers in the area and pollen carried by females and in brood cells was white and composed of myrtaceous grains.

Collection records in the WA Museum indicate that *P. crassipes* forages only at Myrtaceae: *Corymbia calophylla*, *Eucalyptus* and *Melaleuca*. Additionally, I have seen photographs of females on flowers of *M. huegelii* Endl. and *M. lanceolata* Otto courtesy of Kerry Stuart and John Szymanski. All known forage plants are white-flowered.





FIGURES 7–9 *Paracolletes crassipes*. Cocoon: 7) top sectioned across middle, viewed laterally, slightly from above; 8) same viewed slightly from below; 9) enlargement of part of Figure 7 showing layers of unconsolidated silk fibres somewhat teased apart.



FIGURES 10–13 *Paracolletes crassipes*. Cocoon top imaged using a scanning electron microscope: 10) outer surface, central, solidly sealed section; 11) outer surface, open-weave fibres of pale marginal area; 12) outer surface, same immediately adjoining cocoon side wall; 13) open-weave silk fibres forming part of pale area of inner surface.

ASSOCIATED ORGANISMS

Females of the bombyliid fly *Sisyromyia aurata* (Walker, 1849) were observed during my January visits hovering over the nesting area and many appeared to be dropping eggs into the grass and litter. Numerous larvae and pupae likely to be those of this fly were found in burrows during excavation. A tiny fly belonging to an unidentified genus of Phoridae was found in one freshly provisioned cell and 37 tiny maggots consistent with being those of phorids were found in another cell containing pollen. Unfortunately, none of the above dipteran larvae developed into adults.

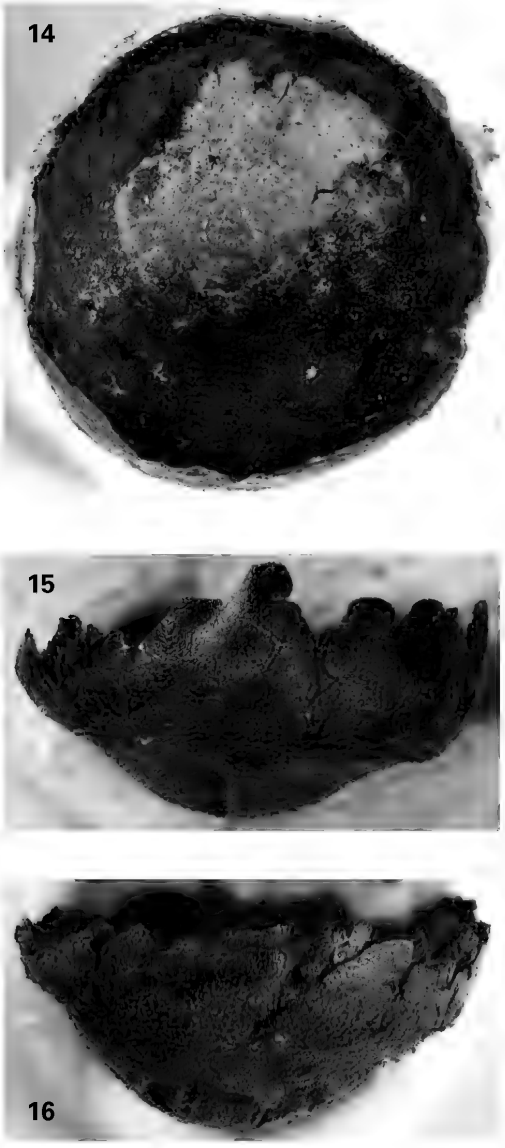
Two adults of a meloid beetle (*Australozonitis* sp.) were found at the excavation site, one dead on the ground and one live in the pit. As well, two coarctate larvae found in brood cells lacking cocoons were typical of Meloidae. Lumps of black material adhering to the cell walls close to the mouth of one such cell were composed of pollen grains consistent with being those of *Eucalyptus*.

DISCUSSION

Judging by the large number of old, soil-filled cells and cocoons recovered during excavation, the nesting site was a perennial one. The absence of tumuli of any significant size at nest entrances might suggest reuse of old burrows. Most nest entrances observed were hidden among short grass and moss and under leaf-litter, although a few were observed in bare ground. It is a moot point whether females select such places to commence new burrows or whether vegetation grows over a previously bare nesting area in which burrow reuse is occurring. Certainly, hidden nest entrances are known for some neopasiphaeine bees (formerly Paracolletini) (Houston 2020).

An unusual feature of male behaviour was that, on hot days, mate-seeking flights were confined to shaded areas of the nesting ground, whereas on cool days, males searched both shaded and sun-lit areas. Evidently, temperature was the controlling factor rather than light

intensity. Many New World diphaglossine bees are adapted for dim-light or nocturnal foraging (Wcislo and Tierney 2009) but *P. crassipes* is clearly diurnal, flying throughout the day. It was notable, though, that many females were observed returning to nests in evening twilight.



FIGURES 14–16 *Paracolletes crassipes*. Meconia: 14) top view of meconium in base of cocoon showing upper layer of whitish, gummy material; 15–16) two meconia removed from cocoons, lateral view (note contours of undersides do not conform completely to rounded bases of cocoons).

At the time of my January visits, the frequency of matings and the number of females searching for nesting sites suggested that a new generation of adults was commencing its nesting cycle, coinciding with a mass flowering of *Corymbia calophylla*. Collection records for *P. crassipes* held by the WAM reveal that in south-western Australia adults are active from December to March. Associated floral visitation records suggest that the bee limits its foraging to a few species of the genera *Eucalyptus*, *Corymbia* and *Melaleuca* (all Myrtaceae). Clearly the species must have more than one generation per year. At Cypress Farm (and in the south-western sclerophyll forests generally) there is a succession of flowering in the order *E. marginata*, *E. patens* and *C. calophylla* (Coleman 1962), covering the bee's flight period.

Only eight of many cocoons collected in January yielded adults and ten cocoons remained intact on 14 December 2020. This is in keeping with knowledge that some prepupae of many solitary bees remain dormant for two or more generations as insurance against poor seasons (Michener 2007).

I was not able to determine the architecture of individual nests because of obstacles such as roots and rock in the soil. However, because freshly made brood cells and occupied cocoons occurred singly, not in clusters, and were distributed through at least 50 cm of the soil profile to a depth of 85 cm, I infer that females construct their cells singly at well-separated intervals along their shafts. This is the pattern recorded for certain diphaglossines in the genera *Diphaglossa* Spinola, *Ptiloglossa* Smith and *Zikanapis* Moure (= *Caupolicana* Spinola) (Roberts 1971; Rozen 1984; Sarzetti et al. 2013). Nest architecture of neopasiphaeines is poorly documented but lateral burrows of some species radiate from the lower end of the shaft (Michener 1960; Houston and Maynard 2012) while those of *Lonchopria cingulata* are concentrated about the shaft's lower extremities (Michener and Lange 1957).

The formation of soil nodules around older brood cells is not unique to *P. crassipes*, having been observed also in the diphaglossine *Caupolicana yarrowi* (Cresson) (Rozen et al. 2019), the neopasiphaeine *Trichocolletes orientalis* Batley and Houston (Houston 2020) and some Stenotritidae (Houston 1984; Houston and Thorp 1984; Houston 1987). In the case of *C. yarrowi*, Cane and Rozen (2019) found evidence that females impregnate their cell walls with nectar, enabling them to trowel them to a smooth finish prior to applying a waterproof lining. Perhaps this behaviour is widespread among burrowing bees.

Diphaglossinae exhibit some characteristics of nesting biology that distinguish them from other hairy colletids (Rozen 1984; Sarzetti et al. 2013; Sarzetti et al. 2014): cells are vertically oriented, have strongly curved necks that are varnished like the remainder of the cell walls and are closed by a cell plug that is thin and

situated in the curved neck (a conspicuous exception is *Cadeguala occidentalis* (Haliday) which builds a thick plug in the cell mouth (Torchio and Burwell (1987)); the larval provision is partly liquid; mature larvae spin cocoons; and the cocoons have a flat top. *Paracolletes crassipes* shares most of these characteristics but appears not to construct a cell plug (unless the smooth inner end of the barricade filling the lateral burrow equates to a plug).

Some Australian Neopasiphaeinae, notably *Anthoglossa* Smith and *Trichocolletes* Cockerell, also construct vertical brood cells and have a liquid provision, but none is known to construct curved, varnished cell necks or larval cocoons (Houston 2018, 2020). Comparison of nesting biology across taxa of hairy colletids is hampered because information is lacking for some key groups: (a) *Anthoglossa*, treated as a subgenus of *Paracolletes* by Michener (1965, 2007); (b) the diphaglossine tribe Dissoglottini (particularly the genus *Mydrosomella* Michener which contains small species 'with the superficial appearance of some Paracolletini' (Michener 1986b).

Diphaglossinae are the only Colletidae known to construct cocoons according to various authors (Michener 2007; Almeida 2008; Danforth et al. 2019). However, Michener and Lange (1957) recorded finding prepupae of the Brazilian bee *Colletes michenerianus* Moure, each enclosed in 'a very thin, light brown cocoon made up of fibers, with the spaces between the fibers filled with pale brown amorphous material. The cocoon was constructed against and adhered to the cellophanelike material of the nest except where feces were between the cocoon and the nest material'. The significance of their find was apparent to the authors who remarked that 'This is the only *Colletes* that we know that constructs a cocoon.' To my knowledge, this record has not been refuted.

Cocoon spinning is regarded as a plesiomorphic character state within the Hymenoptera and has been lost independently in various groups of bees (Rozen 1984; Radchenko and Pesenko 1996; Michener 2007; Almeida 2008; Danforth et al. 2019). Furthermore, cocoons may be spun by one generation of a species and not another, or the form of the cocoon may vary between generations (Mello and Garófalo 1986; Rozen 1993). Clearly, cocoon spinning is a habit that is easily 'switched off' or modified. Consequently, we should be wary of attaching too much significance to its presence or absence in establishing relationships among taxa. However, certain features of a cocoon might be considered derived and therefore of more use in phylogenetics. The cocoons of Diphaglossinae (including *Paracolletes*) differ from those of other bees in their flat tops. Rozen (1984) recognized three distinct layers in the cocoon tops of several New World diphaglossines: the flat outermost layer ('operculum') which was parchment-like but fenestrated, the concave innermost layer ('ceiling'), also parchment-like and fenestrated and, between these two, a zone of varying thickness filled with loosely woven silk ('filter'). Such an arrangement was presumed by some authors (e.g. Roberts 1971; Rozen 1984) to permit gaseous exchange between the cocoon lumen and the soil. The cocoon top of *P. crassipes* is a thinner, more solid structure, with the operculum and ceiling lacking fenestrations and being separated from one another by laminae but no air spaces. Presumably, the acentric patch of densely woven, multilayered and unsealed silk fibres in the cocoon top of *P. crassipes* equates to the filter of New World diphaglossines and serves the same purpose.

Among various cocoon-spinning bees, differences occur in the timing of defaecation with respect to cocoon spinning so that faeces may remain external to the cocoon, become incorporated in its outer walls or be enclosed within the cocoon (Stephen et al. 1969; Rozen 1984, 1993; Danforth et al. 2019). In most New World diphaglossines studied to date, faeces are deposited in the bottom of the cell as a solid mass (meconium) when the cocoon is only partially constructed. In some cases, the walls of the cocoon do not extend to the base of the cell, while in other cases they do, but in a more porous form. Then, once the meconium has been formed, the larva lays a parchment like layer over its top to form the floor of the cocoon (Rozen 1984). In *Cadeguala occidentalis*, a thin, cup-shaped meconium is sealed between inner and outer cocoon layers (Torchio and Burwell 1987). Larvae of *P. crassipes* behave differently, defaecating only upon completion of the cocoon and not covering the meconium with any spun material. Mature larvae of apoid and vespoid wasps behave similarly (Evans and Eberhard 1973; Gess 1996) and this behaviour must therefore be viewed as plesiomorphic.

A clear liquid or a white, gummy material left when the liquid dries was found in many cocoons of *P. crassipes*. These substances were likely to be products of the Malpighian tubules of final instar larvae, given the presence of urate bodies in the dried material. Mature larvae of the diphaglossine *Crawfordapis luctuosa* Smith also deposit clear liquid on top of their faecal masses (Roubik and Michener 1985) and Rozen (1984) surmised that the larvae were eliminating water ingested with the liquid provisions. It is pertinent to note, therefore, that the larval provision of *P. crassipes* also has a significant liquid component. Larvae of Neopasiphaeinae are not known to produce liquid waste, but those of *Colletes ciliatoides* Stephen (Colletinae *sensu* Almeida et al. 2018) produce a clear gel-like material from the anus and spread it over the faecal mass where it dries like a varnish (Torchio 1965).

The need to rid cells of excess water contained in faeces is believed by Rozen (1984) to have led to an interesting behaviour in mature larvae of some New World diphaglossines (*Cadeguala* and *Ptiloglossa* species): they perforate or destroy the CLM lining of the bottoms of their cells with their mandibles before

completing their cocoons, allowing water from wet faeces to soak into the soil. No such perforation was observed for *C. luctuosa* or *P. crassipes* and their cocoon bottoms are impermeable.

In summary, the observations recorded in this study are largely consistent with the current (Almeida et al. 2018) placement of *Paracolletes crassipes* in the Diphaglossinae. So, it is confounding that adults of *P. crassipes* do not key to this subfamily. The diagnostic features of Diphaglossinae have changed over time along with the concept of the taxon (e.g. Michener 1966, 1986b, 2007) and in Michener's (2007) key to subfamilies of Colletidae, the Diphaglossinae are distinguished from other hairy colletids by just two characteristics: (1) stigma much reduced; (2) glossa deeply bifid with the apical lobes directed apicolaterally. *Paracolletes* has a very small stigma (as do some other hairy colletids including the Australian taxa *Anthoglossa, Hesperocolletes* Michener and *Trichocolletes*) but its glossa is not at all bifid. Relative size of the stigma alone is not a reliable taxonomic character for, as Danforth (1989) demonstrated, it is inversely proportional to body size across a range of bee taxa.

ASSOCIATED ORGANISMS

Circumstantial evidence gathered during this study points to a parasitic association between the moderately large bee fly, *Sisyromyia aurata*, and *P. crassipes*. Larvae and pupae presumed to be of this fly seemed to be very mobile and several dropped out of the walls of my excavation, but none was observed in a brood cell of the bee. Perhaps it is their depredations that account for the considerable number of empty cells observed.

A more definite parasitoid was a meloid species, coarctate larvae of which were found resting in brood cells.

It was surprising that no hymenopteran parasitoids such as gasteruptiids, mutillids or ichneumonids (especially *Labium*) were found to be associated with nests of *P. crassipes*. They are frequently found in association with other Australian ground-nesting bees.

The exceptionally tough cocoon top of *P. crassipes* might explain why some occupants (presumably parasitoids) had exited through the cocoon side walls.

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Revision of *Lucasium stenodactylus* (Boulenger, 1896; Squamata: Diplodactylidae), with the resurrection of *L. woodwardi* (Fry, 1914) and the description of a new species from south-central Australia

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ABSTRACT – The past two decades have seen an increase in the documentation of reptile diversity in the Australian arid zone through a combination of genetic and morphological analyses based on widespread collections. Especially common are descriptions of new species of geckos, mostly from rocky refugia, but also widespread terrestrial species as well. Here we focus on outstanding taxonomic issues with the widely distributed diplodactylid *Lucasium stenodactylus* (Boulenger). We analysed published and newly generated genetic sequences, especially from South Australia, to resolve previous indications from morphology and molecular data that at least two other species may exist within the current definition of *L. stenodactylus*. We found strong support for a Pilbara region species, to which the name *Diplodactylus woodwardi* Fry applies, and for a new species occurring mostly in South Australia, *Lucasium microplax* sp. nov. The Pilbara and South Australian lineages are distinguished on numerous distinctive scalation and pattern characteristics and show deep genetic divergences. The redescription of *L. woodwardi* adds yet another gecko species to the highly diverse Pilbara region reptile fauna, and the description of the South Australian lineage as a separate species from *L. stenodactylus* adds another widespread arid-adapted species to its reptile fauna.

KEYWORDS: Australian arid zone, gecko, molecular genetics, ND2, South Australia

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INTRODUCTION

The Australian arid zone (AAZ) is now recognised as a major area for the generation of diversity (Byrne et al. 2008; Anderson et al. 2016) and especially reptile diversity (Brennan and Oliver 2017). The AAZ harbours the most diverse lizard fauna in the world (Pianka 1986; Powney et al. 2010) and has become a model area for the study of diversification and large-scale evolutionary radiations (Rabosky et al. 2007). Although already noted for its very high species richness, descriptions of species from the AAZ are ongoing at a relatively high rate. Almost all new lizard species descriptions from the AAZ in the past 20 years have involved a combination of morphological and molecular data, with recent additions to the fauna coming from across the range of major squamate taxa that inhabit the region, including agamids (Melville et al. 2019), skinks (Rabosky et al. 2017) and snakes (Ellis et al. 2017; Maryan et al. 2020).

Geckos (Carphodactylidae, Diplodactylidae, Gekkonidae and Pygopodidae) are particularly diverse in the AAZ and knowledge of their diversity and the potential drivers of its evolution has advanced rapidly in recent years (Pepper et al. 2013; Nielsen et al. 2016; Ashman et al. 2018). Most new species of geckos have been described from rocky refugia within the AAZ, especially the Pilbara and Central Ranges (e.g. Oliver

et al. 2010; Pepper et al. 2013; Doughty et al. 2018a), but new species also continue to be revealed in the superficially more homogeneous sandy desert regions (e.g. Maryan et al. 2007; Oliver et al. 2014; Oliver and Doughty 2016).

An early taxonomic synthesis on AAZ geckos was Kluge's landmark 1967 monograph on *Diplodactylus* Gray, 1832 which included a diverse subgroup of largely or completely terrestrial species (excluding the largely arboreal *Strophurus* Fitzinger, 1843) with significant variation across the AAZ (Storr et al. 1990). Since then this terrestrial subgroup has become better understood as a clade of diplodactylid geckos belonging to three genera: *Diplodactylus*, *Lucasium* Wermuth, 1965 and *Rhynchoedura* Günther, 1867 (Oliver et al. 2007). Among these, the genus *Lucasium* is a group of small to medium sized terrestrial geckos, inhabiting much of arid and semiarid Australia, excluded only from the humid south-western, eastern and south-eastern forests. Currently, *Lucasium* includes 12 species (Uetz et al. 2020; Vanderduys et al. 2020), but there is still evidence for unrecognised diversity in the genus.

Within the very wide-ranging *L. stenodactylus* (Boulenger, 1896), morphological evidence from as far back as Kluge's (1967) monograph and more recent molecular data (Pepper et al. 2006) point to the existence of cryptic species in this complex. Kluge's (1967) *Diplodatylus stenodactylus* 'population A' comprised specimens from the western deserts, which included the type locality of *Diplodactylus stenodactylus*, Roebuck Bay, Broome, Western Australia in the north-west of its distribution. Kluge depicted the colour pattern of this population as having small to moderately large pale spots distributed over light reddish-brown dorsal surfaces and limbs, and possessing a vertebral stripe. Other significant morphological features were small apical plates, a reduction from 5 to 4 in the phalanges of the fourth finger and nostril excluded from contact with the rostral scale. In his description of 'population A' from Western Australia, Kluge also included the holotype of *Diplodactylus woodwardi* Fry, 1914 although it was in very poor condition making assessment difficult (Kluge 1963). However, he explicitly excluded specimens of *stenodactylus* collected from the Warburton area, near the border of South Australia and the Northern Territory. He referred these to his 'population B', with the specimens possessing a wide and distinct vertebral stripe and bordered by dark red or brown colouration with large pale spots on the dorsal and lateral surfaces of the body and limbs. Morphologically, these specimens possessed apical plates that were small ('rarely wider than the proximal portion of digit'; p. 1049; illustrated in figure 3I), retained the plesiomorphic count of five phalanges in the fourth finger and the nostril was not in contact with rostral in ~3/4 of specimens.

Lucasium stenodactylus was the subject of a detailed molecular study by Pepper et al. (2006; see also Pepper et al. 2008). They found significant genetic variation in populations from Western Australia, with dense sampling from the Pilbara region and sparser sampling across the state. The Pilbara and Gascoyne regions to the south were a cohesive lineage in the analysis (which they called 'Pilbara'), and to which the name *D. woodwardi* could apply. The three other lineages recovered were 'non-Pilbara' which referred to western desert populations, 'sp. 1' which corresponded to specimens from the Western Australia-South Australia border and 'sp. 2' whose distribution was to the south of the other three lineages. Pepper et al.'s 'sp. 2' was later described as *L. bungabinna* Doughty & Hutchinson, 2008 based on a combination of morphological analysis, the genetic results of Pepper et al. (2006) and an unpublished allozyme study (M. Adams and S. Donnellan, pers. comm.). Although the description of *L. bungabinna* reduced some of the taxonomic ambiguity within *L. stenodactylus*, there remain two major lineages from Pepper et al. (2006), i.e. 'Pilbara' and 'sp. 1', as well as Kluge's 'population A' and 'population B' that require resolution.

Here, we investigate these unresolved populations to further stabilise the taxonomy of *L. stenodactylus*. We sequenced 45 more individuals of the Pepper et al. (2006) 'sp. 1' population from South Australia and 12 more individuals of 'non-Pilbara' *L. stenodactylus*, and provide a morphological analysis of the three main groups considered here: i) true *L. stenodactylus* from the western deserts, ii) the Pilbara region population, for which the name *Diplodactylus woodwardi* potentially applies, and iii) Kluge's 'population B' and Pepper et al.'s 'sp. 1' that occurs widely within arid South Australia and bordering states, which we describe herein as a new species. Although there was some genetic structure among some of the samples from the Australian monsoonal tropics from Pepper et al. (2006), the available samples are insufficient to resolve the wide variation in morphology observed in this region, hence our focus here is largely on the three major arid zone populations of what are currently regarded as *L. stenodactylus*.

MATERIALS AND METHODS

DNA AMPLIFICATION AND SEQUENCING

We collected new NADH Dehydrogenase Subunit 2 (ND2) sequence data for 47 individuals and these were added to data generated in Pepper et al. (2006) and Pepper et al. (2008) (see Appendix for specimen information and GenBank accession numbers). We included multiple additional taxa in order to put the putative new taxon in genetic context with the other members of the genus *Lucasium*. Detailed information on DNA extraction and sequencing protocols for all three loci used in this study are outlined elsewhere (Pepper et al. 2006). In brief, DNA from new samples was obtained using the EDNA HiSpEx tissue kit (Chaga) following the manufacturers protocol. The ND2 region was amplified and sequenced in three overlapping fragments, using the forward primer L4437 (5'-AAGCTTTCGGGGCCCATACC-3';

Macey et al. 1998) and the reverse primer tRNA Asn (5'-CTAAAATRTTRCGGGATCGAGGCC-3'; Read et al. 2001). A modified version of L4882 (5'-CAACCTGACAAAAAHTHGCMC-3'; Macey et al. 2000) was used as an internal sequencing primer. PCR products were amplified for 37 cycles at an annealing temperature of 60°C. Purified PCR products were run on an ABI 3100 auto-sequencer. All genes were sequenced from both 3' and 5' ends separately.

ANALYSIS OF SEQUENCE DATA

New ND2 sequences generated in this study were aligned with data presented in Pepper et al. (2006) and Pepper et al. (2008) in Geneious Prime 2020 1.1. We translated nucleotide data into amino acid sequences and checked the alignment for internal stop codons and frame-shift mutations. In addition to ND2, we also collated data from the aforementioned studies that included a portion of the 16S ribosomal RNA and a portion of the protein-coding locus RAG1. Following the removal of ambiguously aligned nucleotide sites, the final ND2 dataset consisted of 1051 base-pairs (bp), 16S consisted of 484 bp and RAG1 consisted of 834 bp, totalling 2369 bps for the concatenated dataset. Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian methods. For the likelihood analysis we concatenated the data and partitioned the combined dataset by gene. We used the RAxML plugin in Geneious, implemented the general time-reversible substitution model with gamma-distributed rates among sites (GTR + G). We used *Diplodactylus fulleri* Storr, 1978 to root the phylogenetic tree. Bootstrap support was determined using 1000 replicates. Bootstrap values above 80 are considered as providing strong nodal support.

In addition to our concatenated ML approach, we used the hierarchical model implemented in starBEAST2 v. 2.6.3 (Ogilvie et al. 2017). The phylogenetic signal was limited in the 16S and RAG1 loci (visible in figure 3 of Pepper et al. [2006], and also corroborated in RAxML analyses of individual loci in our study, not shown) so we used the concatenated dataset for this analysis as well, using the HKY substitution model, employing a strict clock, and using a Yule tree prior. We conducted two separate runs, with samples drawn every 10,000 steps over a total of 100,000,000 steps, with the first 10% discarded as burn-in. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using the diagnostic software Tracer v1.5 (Rambaut and Drummond 2007). Effective sample sizes were well above 200 for all parameters. Both runs produced the same topology with very similar posterior probabilities, so we combined runs to generate a single consensus tree. Posterior probabilities above 90 were considered as providing strong nodal support.

MORPHOLOGY

We examined specimens, including type material, held at the Western Australian Museum, Perth (WAM), Northern Territory Museum, Darwin (NTM) and the South Australian Museum, Adelaide (SAMA). Type specimens were examined from WAM, Natural History Museum, London (NHMUK, formerly BMNH) and Zoolgisk Museum, Universitetets Oslo, Oslo, Norway (UZMO). Specimens measured are listed and denoted as such in the Appendix.

For the morphological measurements, we sorted specimens based on the genetic results of Pepper et al. (2006) and original sequences presented here. We chose a subset of well-preserved adult specimens for measuring with most specimens genotyped. Several smaller specimens were measured (<43 mm snout-vent length), but these were excluded from statistical summaries except for scalation counts. Colouration was determined from photographs of live individuals or recently collected specimens.

The following measurements were recorded to the nearest 0.1 mm using digital callipers and dissecting microscope: snout-vent length (SVL), from tip of snout to anterior edge of vent; trunk length (TrunkL), from axilla to groin; tail length of original and regenerated tails (TailL), from cloaca to tail tip; tail width (TailW) from widest point of tail; forearm length (ArmL), from elbow to tip of 4th finger; foreleg length (LegL), from upper surface of knee to tip of 4th toe; head length (HeadL), from tip of snout to posterior margin of the retroarticular process, measured at an oblique angle; head width (HeadW), at widest point; head depth (HeadD) at largest point on crown; orbit length (OrbL), from lower anterior to upper posterior edges of bony socket; naris to eye (NarEye), from naris to anterior corner of eye; snout to eye (SnEye), from tip of snout to inner anterior edge of eye socket; eye to ear (EyeEar), from inside the posterior edge of bony eye socket to anterior margin of ear; internarial distance (INar), from naris to naris; interorbital width (IO), interorbital width at centre of eyes; mental length (MenL), from mouth to posterior edge; mental ratio (MenL/W), ratio of mental length/width; rostral crease length (CreaseL), proportional length of crease from dorsal edge of rostral scale.

The following scalation data were recorded and scored under a dissecting microscope: supralabial scales (SupLab), infralabial scales (InfLab), anterior supranasals (AntSup) and precloacal pores (Pores). Sex was determined by the presence of enlarged cloacal spurs, cloacal bulge and/or everted hemipenes (males) or by follicles and eggs (females).

RESULTS

MOLECULAR GENETICS

Our RAxML phylogeny (Figure 1) includes all the Western Australian members of the genus *Lucasium*, as well as the two Western Australian *Rhynchoedura* species and *Diplodactylus fulleri*. Within *Lucasium*, two main clades were recovered. A well-supported clade with taxa distributed largely in southern Western

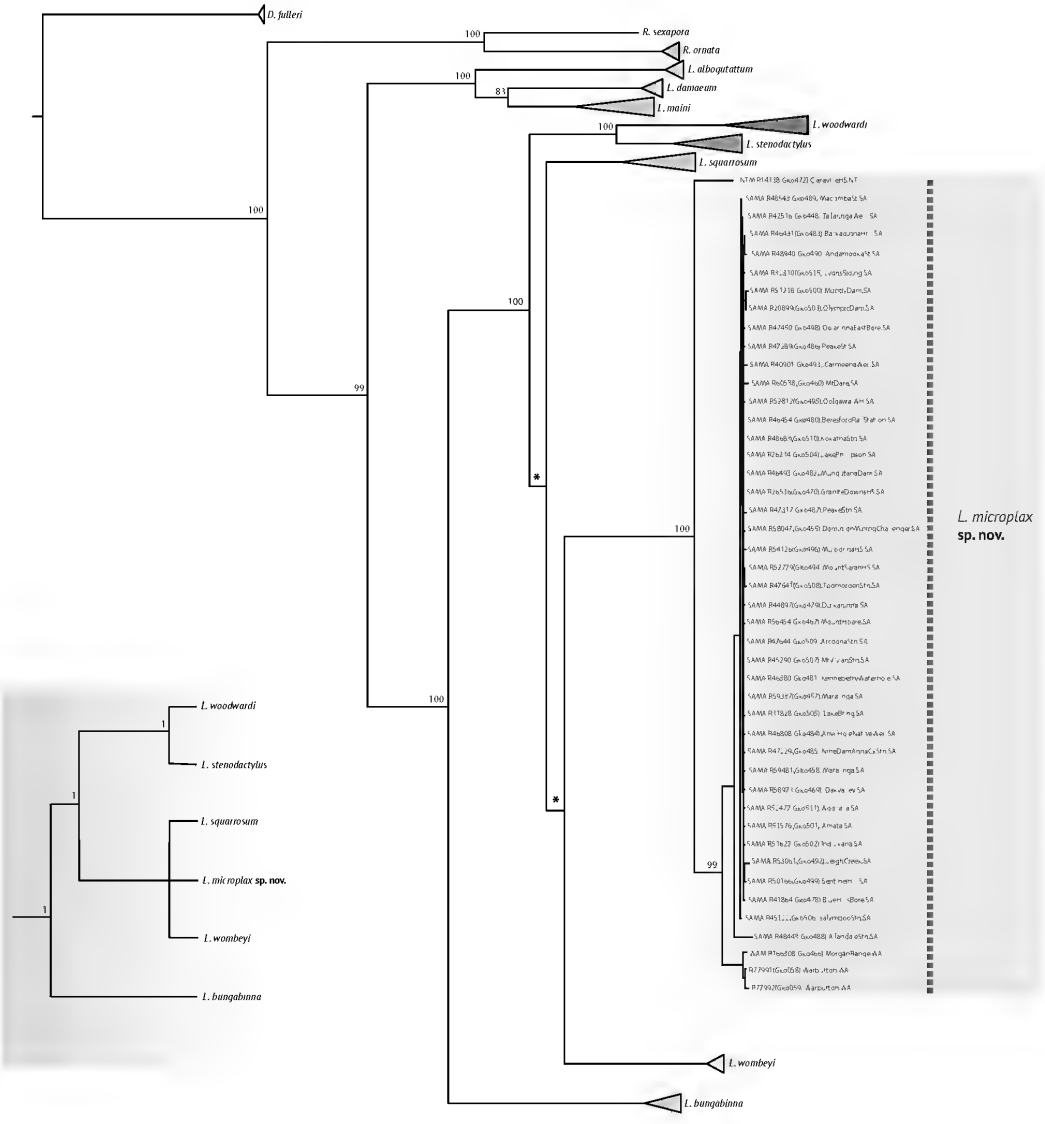

FIGURE 1 Phylogram of major lineages of *Lucasium* in the western arid zone. Names for lineages within the *L. stenodactylus* species complex referred to in the text: *L. stenodactylus*, northern lineage; *L. woodwardi*, Pilbara lineage; *L. microplax* sp. nov., South Australian lineage. * = BP support <50.

Australia comprises *L. alboguttatum* (Werner, 1910) and the sister taxa *L. damaeum* and *L. maini*. The second clade included the more northerly distributed species; however, within this clade, relationships among *L. stenodactylus*, the Pilbara lineage of *L. stenodactylus* (i.e. *L. woodwardi* in Figure 1), the South Australian lineage of *L. stenodactylus* (i.e. *L. microplax* sp. nov. in Figure 1), *L. squarrosum* (Kluge, 1962) and *L. wombeyi* (Storr, 1978) are largely unresolved (Figure 1). Our Bayesian analysis implemented in starBEAST2 also failed to resolve the relationships within this group (see Figure 1, inset). Our analyses expanded on those presented in Pepper et al. (2006) by sequencing tissues from more specimens, especially from South Australia. These additional South Australian individuals grouped together with those labelled 'sp. 1' in Pepper et al. (2006), along with three individuals from Western Australia (WAM R77991, WAM R77992, WAM R166308) and a single individual from the southern Northern Territory (NTM R14338). The 'sp. 1' lineage

is distributed predominantly in South Australia (Figure 2). Uncorrected P-distances calculated in PAUP* v. 4.0a (Swofford 2002) between this South Australian clade (*L. microplax* sp. nov.) and *L. squarrosum* and *L. wombeyi* range from 15–18%, and are between 15–19% between the South Australian clade and *L. stenodactylus*. A deep phylogenetic split (bootstrap 100) separates populations of *L. stenodactylus* from the Pilbara region from those in the western deserts, with uncorrected P-distances between these clades at 11–15%.

In summary, we found that the specimens currently assigned to *L. stenodactylus* fell into three well-supported and potentially species-level clades. One clade ('Northern') includes specimens from near the type locality of *L. stenodactylus* and includes populations extending across much of the northern and central arid areas of Western Australia and east into the Northern Territory (Figure 2). The second ('Pilbara') clade is centred on the arid ranges of the Pilbara and Gascoyne regions of the central west of Western Australia. These two clades are recovered as sister lineages. The third ('South Australian') clade comprises specimens from central and northern South Australia, eastern Western Australia and southern Northern Territory. Although previously included with *L. stenodactylus*, this clade is phylogenetically closer to *L. squarrosum* from the southern inland of Western Australia and *L. wombeyi* from the eastern Pilbara.

MORPHOLOGICAL ASSESSMENT

Table 1 summarises the morphological measurements among the three groups of *L. stenodactylus* considered here. A mensural character that was noticeably different among forms was the shorter original tails of the South

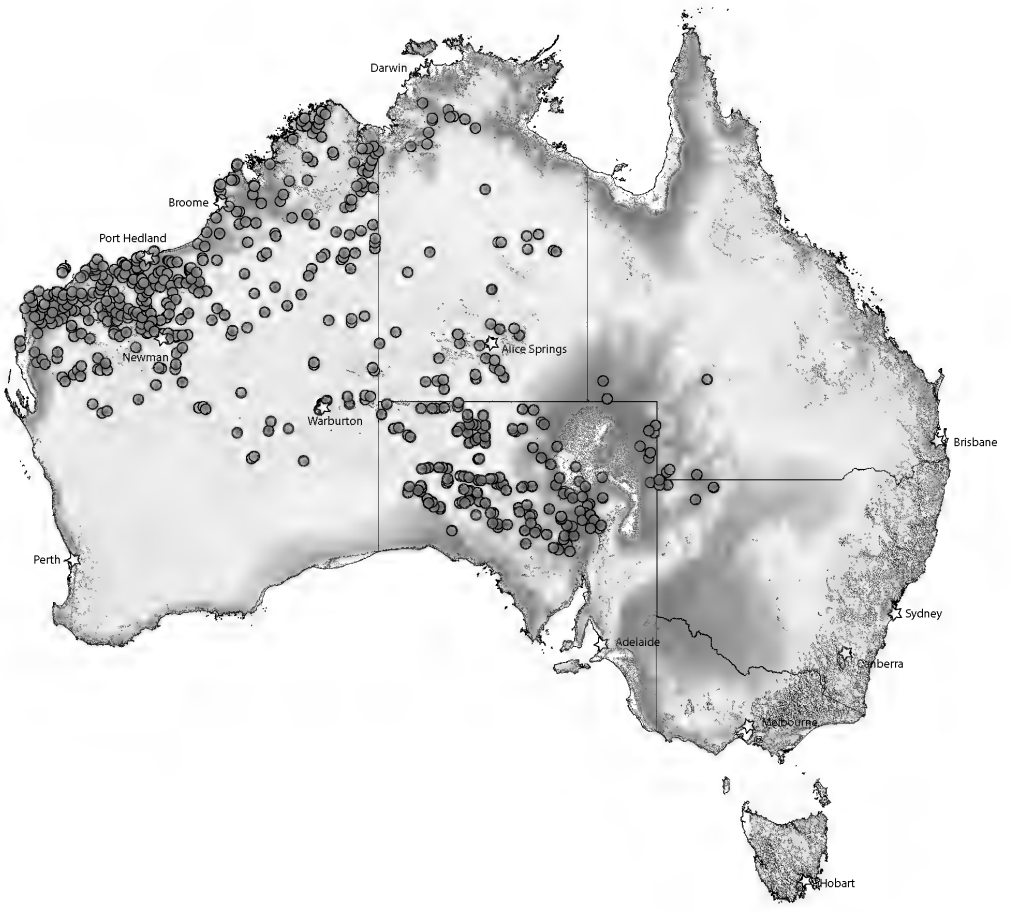

FIGURE 2 Distribution of the *Lucasium stenodactylus* species complex clades in the Australian arid zone. Key: yellow = Northern lineage (*L. stenodactylus*); red = Pilbara lineage (*L. woodwardi*); blue = South Australian lineage (*L. microplax* sp. nov.; Kluge [1967]'s 'population B'; Pepper et al. [2006]'s 'sp. 1').

Australia individuals: the average TailL%SVL was around 80% for Northern and Pilbara populations, but only 70% for South Australian populations. Features of scalation that are informative in separating the three clades include terminal apical plate (scansor) size and shape, rostral scale arrangement, infralabial size and precloacal pores. Northern specimens have small apical plates that were nearly as wide as the digit (Figure 3A). In contrast, Pilbara specimens have expanded apical plates that were wider than the width of the digit (Figure 3B) and visible in dorsal view. Populations from South Australia have very small apical plates that do not exceed the width of the digit and usually fail to contact the base of the claw (Figure 3C). Differences in finger width were also apparent for South Australia populations, with the distal phalanx noticeably narrowing in width (Figure 3C) compared to the other two taxa (Figures 3A, B). The rostral scale is separated from the nostril in the Northern and Pilbara populations (Figure 4A); in contrast, in South Australian populations the rostral is either in point contact with the nostril or only narrowly separated from it (Figure 4B). The mental and infralabial scales in Northern specimens are smaller than the other two lineages, with these scales not extending far onto the gular region (Figure 5A). In contrast, the mental and infralabial scales of specimens from the South Australia clade are relatively large, extending much further on to the gular region (Figure 5C). Pilbara populations are intermediate between these two extremes (Figure 5B).

Precloacal pores also differed among lineages. In Northern and Pilbara clades, there was a range of 2–6 pores, whereas in the South Australia clade there was a consistent pattern of only two pores, the typical configuration in *Lucasium*. There was sexual dimorphism in pore expression as well. In Northern adult males and females, the pattern was typically two pores per side, but occasional three on a side and sometimes zero. Pilbara males also shared this pattern, but interestingly females usually had no pores, or occasionally one or two. In South Australian populations, both males and females almost always had a single pore on each side.

TABLE 1 Summaries of characters and ratios measured for *Lucasium stenodactylus*, *L. woodwardi* and *L. microplax* sp. nov. Mean±S.D. (range). Sample sizes of adults are listed in column headings (with juveniles in parentheses — not used in meristic calculations), and for males and females separately for SVL and TrunkL. Only original tails measured. Samples sizes also provided when they deviate from total N.

Character	*L. stenodactylus* N = 16 (19)	*L. woodwardi* N = 25 (27)	*L. microplax* sp. nov. N = 22 (23)
SVL	Female (N = 8): 49.9±4.1 (44.0–55.0) Male (N = 8): 51.0±3.9 (44.0–56.5)	Female (N = 9): 48.6±1.3 (47.0–50.5) Male (N = 16): 47.4±2.5 (44.0–50.5)	Female (N = 11): 49.0±3.1 (44.0–55.5) Male (N = 11): 47.7±1.2 (40.0–51.5)
TrunkL	Female: 25.9±3.0 (19.3–30.4) Male: 26.2±2.2 (23.2–30.7)	Female: 23.6±1.0 (22.0–24.8) Male: 22.8±1.4 (20.2–25.2)	Female: 24.4±1.8 (21.5–27.5) Male: 22.7±1.9 (19.5–25.5)
TailL	41.4±5.6 (35.0–50.0) N = 13	36.6±2.9 (31.5–40.0) N = 18	33.7±2.3 (28.5–38.0) N = 18
TailW	3.8±0.5 (2.9–4.7) N = 13	3.6±0.5 (2.6–4.4) N = 18	3.7±0.5 (2.9–4.4) N = 19
ArmL	6.3±0.5 (5.4–6.9)	6.3±0.4 (5.4–7.2)	6.4±0.3 (5.7–6.9)
LegL	7.9±0.6 (7.0–8.8)	7.5±0.4 (6.6–8.8)	8.2±0.5 (6.8–8.9)

Character	*L. stenodactylus* N = 16 (19)	*L. woodwardi* N = 25 (27)	*L. microplax* sp. nov. N = 22 (23)
HeadL	13.2±1.1 (10.6–14.8)	12.7±0.8 (11.4–13.8)	12.7±0.8 (10.9–13.7)
HeadW	8.0±0.8 (6.8–9.3)	7.6±0.7 (6.8–9.2)	7.7±0.4 (6.8–8.4)
HeadH	5.5±0.8 (4.1–6.5)	5.3±0.5 (4.2–6.0)	5.6±0.3 (4.9–6.2)
OrbL	3.1±0.4 (2.4–3.9)	3.1±0.2 (2.5–3.3)	3.2±0.3 (2.6–3.5)
NarEye	4.1±0.4 (3.5–4.6)	3.7±0.2 (3.3–4.1)	4.2±0.4 (3.5–4.8)
SnEye	5.0±0.5 (4.0–5.5)	4.7±0.2 (4.4–5.0)	4.8±0.3 (3.9–5.3)
EyeEar	4.3±0.4 (3.4–4.9)	3.9±0.3 (3.4–4.3)	3.6±0.2 (3.0–3.9)
INar	1.6±0.3 (1.1–2.0)	1.3±0.1 (1.2–1.4)	1.3±0.2 (1.0–1.5)
IO	3.9±0.4 (3.1–4.3)	3.3±0.3 (2.9–3.9)	3.6±0.3 (3.0–4.0)
SupLab	9.4±1.1 (8–12)	9.3±0.6 (8–10)	9.3±0.9 (8–10)
InfLab	10.2±1.0 (9–12)	10.0±0.8 (9–12)	9.5±1.0 (8–12)
CreaseL	0.24±0.22 (0–0.60)	0.30±0.20 (0–0.75)	0.21±0.16 (0–0.50)
AntSup	5.3±0.6 (4–6) N = 17	4.6±0.6 (4–6)	4.6±0.8 (4–7)
MenL	1.14±0.17 (0.93–1.40)	1.12±0.16 (0.96–1.38)	1.27±0.16 (0.85–1.57)
MenL/W	1.13±0.16 (0.82–1.44)	1.24±0.15 (0.99–1.48)	1.20±0.18 (0.97–1.54)
Tail%SVL	0.81±0.4 (0.73–0.88) N = 13	0.77±0.04 (0.68–0.83) N = 18	0.70±0.03 (0.64–0.78) N = 18
HeadL/SVL	0.26±0.01 (0.23–0.27)	0.27±0.01 (0.24–0.30)	0.26±0.02 (0.23–0.30)
HeadW/SVL	0.16±0.01 (0.13–0.17)	0.16±0.01 (0.14–0.18)	0.16±0.01 (0.15–0.17)
HeadH/SVL	0.11±0.01 (0.09–0.13)	0.11±0.01 (0.09–0.13)	0.12±0.01 (0.10–0.12)

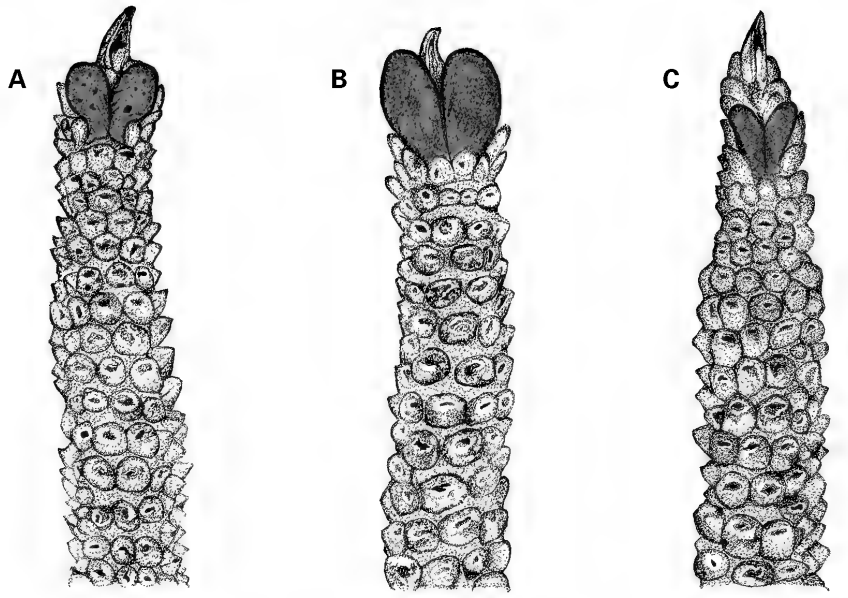

FIGURE 3 Ventral surfaces of the 4th toe of the *Lucasium stenodactylus* species complex. A) Northern lineage (specimen NTM R6299); B) Pilbara lineage (WAM R127703); C) South Australian lineage (SAMA R53061). Terminal plates highlighted in red to show relative differences in size. (Illustrations J. Eastwood.)

FIGURE 4 Two different scale configurations on the surface of the snout tip of *Lucasium stenodactlyus* species complex members. A) Northern (illustrated specimen, WAM R84551) and Pilbara lineages; B) South Australian lineage (SAMA R53061). Rostral scale highlighted in green to show separation (A) or point contact (B) with nostril. (Illustrations J. Eastwood.)

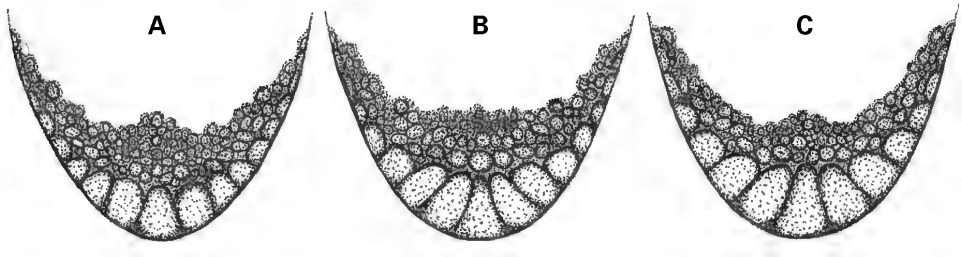

FIGURE 5 Chin of *Lucasium stenodactylus* species complex lineages, showing the relatively small mental and infralabial scale sizes typical of *L. stenodactylus*. A) Northern lineage (WAM R157948); B) Pilbara lineage (WAM R113591); C) South Australian lineage (holotype, SAMA R48940). (Illustrations J. Eastwood.)

Dorsal pattern and colouration differed consistently among all three lineages, although there was wide variation within taxa and moderate overlap among them. The basic pattern, common to all three clades considered here, was a red to brown background colour with usually a narrow pale vertebral stripe with small to moderate spots or blotches on the sides (Figures 6–7). The Northern lineage had a lighter overall appearance, with the vertebral stripe always present and with dark variegations overlain on the background pattern; spots were typically small but frequently joined together, especially towards the forebody (Figures 6A–B, 7A). In the Pilbara lineage the background colour was a rich reddish-brown; the vertebral stripe was variably expressed, including completely absent, and the small spots tended to be discrete (Figures 6C–D, 7B). In the South Australia lineage, the appearance was also darker, with a more solid brown background colour; the vertebral stripe was always present and clearly defined with black margins; spots tended to be larger and often connected with the vertebral stripe (Figures 6E–F, 7C).

TAXONOMIC CONCLUSIONS

We found minor morphological differences among lineages, and strong genetic and distributional evidence that indicates there are three lineages that are currently combined as *Lucasium stenodactylus*. The type of *Diplodactylus stenodactylus* was collected by K. Dahl during the Mjöberg Expedition from Roebuck Bay (Broome), Western Australia. Specimens from this area

FIGURE 6 Photographs in life of members of the *Lucasium stenodactylus* species complex. A) Northern lineage, Lake Disappointment, Western Australia; B) Northern lineage, Empress Springs, Western Australia; C) Pilbara lineage, Upper Carawine Gorge, Western Australia; D) Pilbara lineage, Balla Balla, Western Australia; E) South Australian lineage, Stuart Creek, South Australia; F) South Australian lineage, Owen Springs, Northern Territory. (Images A–B: B. Maryan; C–D: R.J. Ellis; E: M.N. Hutchinson; F: A. Fenner.)

are part of the Northern lineage genetically (Figures 1–2). The type specimen UZMO 2001 (Figure 8), a subadult male, also corresponded morphologically with specimens from the western deserts (cf. Figures. 7 vs. 8). Therefore, we regard the Northern form as true *L. stenodactylus*.

Ellis et al. (2018) presented a photograph of the holotype of *Diplodactylus woodwardi* Fry, 1914 (WAM R14370; formerly 9876) and provided an account of its collection by J.B. Cleland from the Strelley River in the north-western Pilbara region in 1907. We have sequenced specimens from the Strelley River crossing near Port Hedland (e.g. WAM R102053, WAM R145566; see Pepper et al. [2008]) and all belong to the Pilbara clade. The holotype is a juvenile in extremely poor condition, but we can discern some of the diagnostic morphological features discussed above such as dorsals and ventrals of similar size, enlarged labial scales, narrow toes and overall resemblance in head, body and limb proportions, all of which are consistent with the morphology of the Pilbara clade. Hence, the Pilbara region lineage should be regarded as *L. woodwardi*.

For the South Australian lineage of *L. stenodactylus*, there is no available name. Therefore, we describe this lineage as a new species below.

SYSTEMATICS

Family Diplodactylidae Underwood, 1954

Genus *Lucasium* Wermuth, 1965

Lucasius Kinghorn, 1929: 77 (junior homonym of *Lucasius* Kinahan, 1859 and *Lucasius* Dours, 1872).

Lucasium Wermuth, 1965: 100.

TYPE SPECIES

Ceramodactylus damaeus Lucas & Frost, 1896, by monotypy (as *Lucasium damaeum* Wermuth, 1965)

REMARKS

We follow the expanded concept of *Lucasium* outlined in Oliver et al. (2007) as a genus of the Diplodactylidae (sensu Han et al. 2004) distinguished from all Australian diplodactylids except for *Diplodactylus* and *Rhynchoedura* by having both lateral and medial pairs of cloacal bones. It is distinguished from *Diplodactylus* and *Rhynchoedura* by the reduced or vestigial jugal and medial expansion of the suborbital portion of the maxilla. Further distinguished from *Diplodactylus*, by low numbers of precloacal spinose scales (generally 2–5), presence of precloacal pores (usually one left and one right) in males (absent in *L. byrnei* (Lucas & Frost, 1896), *L. maini* (Kluge, 1962), *L. occultum* (King, Braithwaite & Wombey, 1982) and *L. steindachneri* [Boulenger, 1885]) and by more gracile, elongate proportions of the body, limbs and tail; fourth toe of hind foot approximately seven times as long as wide, tail narrow and moderate to long (70% to 110% of SVL). Further distinguished from *Rhynchoedura* by lower presacral vertebral count (mode 26 versus mode 27), more robust skull, absence of beak-like projecting mental and rostral scales, moderately large labial scales and absence of large precloacal pores (Greer 1989).

Some remarks on the generic and specific endings of names are warranted here. The genus *Lucasium* began as *Lucasius* (Kinghorn 1929), coined for naturalist Arthur H. S. Lucas, one of the describers of the type species (and at the time only species), *Ceramodactylus damaeus* (Lucas & Frost 1896). Owing to *Lucasius* being a junior homonym twice over (see synonymy above), Wermuth (1965) emended the ending to *Lucasium*. As proposed the name *Lucasius* would have been masculine in gender, but the emendation to *Lucasium* changed this to a neuter ending. The endings of several species in *Lucasium* that were transferred from *Diplodactylus* by Oliver et al. (2007) were emended to agree with the neuter gender of *Lucasium*. For the species *L. alboguttatum*, *L. damaeum*, *L. immaculatum*, *L. occultum* and *L. squarrosum*, the specific names can all be interpreted as adjectives and so the endings have been emended correctly. Oliver et al. (2007) also emended the spelling of *stenodactylus* to *stenodactylum*. Boulenger (1896), in describing *Diplodactylus stenodactylus*, did not indicate whether he considered his specific name to be an adjective or a noun. The name translates as 'narrow finger' (noun) rather than 'narrow-fingered' (adjective; e.g. *stenodactylatus*), and so we suggest that the emendation by Oliver et al. (2007) was unnecessary as a noun does not have to agree in gender with the generic name. Accordingly, under Article 31.2.2 under the ICZN Code, we regard *stenodactylus* as a noun in apposition and conserve the original spelling; hence — *Lucasium stenodactylus*.

Lucasium stenodactylus (Boulenger, 1896)

Western sandplain gecko

Figures 3–8

SYNONOMY

Diplodactylus woodwardi Fry, 1914: 175 (fide Kluge 1963)

Diplodactylus stenodactylus stenodactylus Underwood 1954

Lucasium stenodactylum Oliver et al. 2007

Lucasium stenodactylus Swan et al. 2017; this work

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia*:** UZMO K2001, subadult male, collected from Roebuck Bay (Broome), by K. Dahl.

See Appendix for additional material examined.

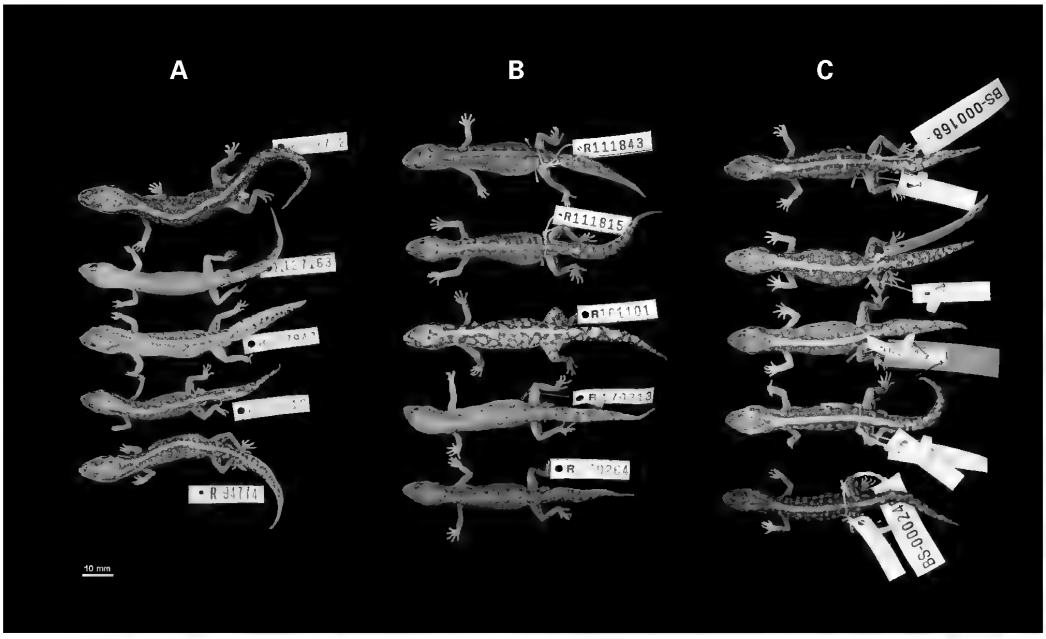

FIGURE 7 Dorsal view of series of preserved specimens of the *Lucasium stenodactylus* species complex. A) Northern lineage; B) Pilbara lineage; C) South Australian lineage.

FIGURE 8 Photographs of the holotype of *Diplodactylus stenodactylus* Boulenger (ZMO 2001) from dorsal, ventral, lateral head and fourth toe tip. The tag with the specimen also shown. (Images A.-H. Rønning, K. Sund and Øystein Wiig, UZMO.)

DIAGNOSIS

A *Lucasium* distinguished from other members of the genus by rostral excluded from nostril, rostral crease present, terminal apical plates approximately the same width as digits, tail moderately long (TailL%SVL ~0.81), males and females with 2–5 precloacal pores and males with a single enlarged cloacal spur. Background colour light reddish brown, overlain by dark variegations, small pale spots tending to join together on forebody and pale vertebral stripe that forks strongly on the nape.

DESCRIPTION

Table 1 presents a morphological summary. Body cylindrical with flat venter; head triangular, narrowing to rounded snout tip; eyes large; loreal region concave; moderate adductor muscles; ear opening small and circular; limbs gracile; five fingers and toes; tail long and tapering to fine point.

Rostral rectangular with crease extending from dorsal edge; rostral separated from nostril; two enlarged supranasals with rounded edges in narrow contact or separated by an internasal; enlarged upper and lower labials, approximately twice as wide as high; first supralabial twice the height of second; scales on snout slightly enlarged; posterior edge of eyelid with short row of spinose scales; mental squarish and flanked by three moderately large infralabials on each side, decreasing in size posteriorly (Figure 5A); gular scales decreasing in size, becoming granular on throat.

Scales on body juxtaposed, rounded with apex posteriorly; scales on venter juxtaposed and slightly rounded; single enlarged cloacal spur on each side of tail; precloacal pores usually 3–6; scales on tail square and flattened, occurring in regular rows; digits covered in fine scales, subdigital scales slightly enlarged; digits only slightly narrowing towards claw; paired terminal apical plates approximately similar width as digit.

Pattern and colour. In life (Figures 6A–B), background colour light reddish brown, overlain with dark complex reticulated variegations extending to limbs; pale cream vertebral stripe with straight to slightly wavy well-defined edges; background with small scattered pale spots, often darkly edged; vertebral stripe forks at neck, continuing anteriorly above and through eye and continuing along canthus as pale streak to tip of snout; top of head with irregular defuse pale blotches often forming a pale cap; margins of eyelid highlighted with sulphur or yellow pigmentation; on lateral surfaces of body, a series of larger pale spots, surrounded by a halo of bordering pigmentation; larger blotches irregular, often joining adjacent blotches; blotches tending to form a lateral line anteriorly, often extending to below ear, connecting with gular region; dorsal region of tail either a continuation of straight-edged vertebral line or a series of pale blotches; ventral surfaces pale cream. Kimberley specimens tend to have a more amoeboid pattern of irregular blotches, with the vertebral stripe less defined. In preservative, the reddish hues are lost, becoming brown (Figure 7A). Older specimens can be quite faded.

HABITAT

Occurs largely on sandplains with spinifex, but also other open areas such as red sandy loams, rocky and alluvial plains and claypans. In the Kimberley region, occurs in woodlands with lateritic or sandstone surfaces, and also sandy and clayey substrates that are more typical of desert populations.

DISTRIBUTION

Most confirmed specimens of this species are from the western deserts in Western Australia, from the type location in the western Kimberley near Broome and extending north into the Dampier Peninsula in the eastern Kimberley, extending south to the east of the Pilbara to near Meekatharra and inland of Shark Bay, then east to near north-eastern South Australia and north again to the Tanami and Kimberley region (Figure 2). Appears to be widespread in the Northern Territory but does not extend into South Australia, Queensland or New South Wales.

COMPARISON WITH OTHER SPECIES

True *L. stenodactylus* can be separated from its congeners based on several morphological characters. It has dorsal scales of similar size as on the venter (vs. dorsals larger on *L. squarrosum*) with dorsal scales uniform (vs. scattered raised tubercles on *L. byrnei*). It differs by possessing small apical plates (vs. absent in *L. damaeum*). For precloacal pores, *L. stenodactylus* typically has 4–6 (occasionally 0–3), *L. woodwardi* 0–5, whereas *L. byrnei*, *L. maini*, *L. occultum* and *L. steindachneri* have none, with the other species typically having two. The rostral does not contact the nostril in *L. stenodactylus* as well as in *L. byrnei*, *L. immaculatum* (Storr, 1988), *L. steindachneri* and *L. woodwardi*, and is variable in *L. occultum* and *L. squarrosum* and in contact in the other species. In *L. stenodactylus* and other congeners the terminal apical plates are approximately as wide as the width of the finger, except the plates are much larger in *L. bungabinna*, *L. byrnei*, *L. occultum*, *L. wombeyi* and *L. woodwardi*, and much smaller in *L. maini* and *L. microplax* sp. nov. and absent in *L. damaeum*.

In addition to these morphological characters, *L. stenodactylus* has a strong vertebral stripe, shared also by *L. bungabinna*, *L. immaculatum* and *L. microplax* sp. nov, whereas the other species tend to have irregular blotches on the dorsum. In contrast to the species with strong vertebral stripes, *L. stenodactylus* possesses a complex pattern of small to medium-sized spots on the side, whereas the other species tend to have a plainer background pattern with the spots in higher relief.

Lucasium stenodactylus is most closely related to *L. woodwardi*, and this is reflected in their resemblance. The most reliable way to distinguish between these species is size of the apical plates. In *L. stenodactylus*, the plates are relatively small and are only in contact proximally, giving a butterfly-like appearance. In contrast, in *L. woodwardi* the paired terminal plates are larger, protruding past the digit and in longer contact with each other where they join (Figure 3). Pattern also

differs, with *L. stenodactylus* usually having a strong vertebral stripe, although this is more variably expressed in the Kimberley region. In addition, *L. woodwardi* can also possess a vertebral stripe, but it is usually less well-defined (Figures 6–7).

REMARKS

Although *L. stenodactylus* has a relatively uniform appearance in the arid zone, specimens from the Kimberley of Western Australia and Top End of the Northern Territory tend to have a more complex pattern with a more weakly-defined vertebral stripe. Pepper et al. (2006) presented evidence of more complex genetic structure of the 'non-Pilbara' (= true *stenodactylus*) populations compared to the 'Pilbara' (= *woodwardi*) populations, suggesting the more uniform habitats of the arid zone have promoted greater genetic homogeneity compared to the Pilbara. Further sampling of *L. stenodactylus* across its range may reveal more complexity in the northern regions, but genetic sampling is not sufficient at present to evaluate this hypothesis.

The revised distribution of this species confines it to only Western Australia and the Northern Territory. *Lucasium stenodactylus* is not known to occur in South Australia, south-western Queensland or north-western New South Wales where it is replaced by the new species. In addition, records of *L. stenodactylus* from north-western Queensland have been reidentified to other *Lucasium* species (unpublished data; see also Vanderduys et al. [2020]).

***Lucasium woodwardi* (Fry, 1914)**

Pilbara ground gecko

Figures 3–7

SYNONOMY

Diplodactylus polyophthalmus Gunther, 1867 (partim)

Diplodactylus stenodactylus Loveridge, 1934

Diplodactylus woodwardi Glauert, 1956

Diplodactylus stenodactylus Wermuth, 1965

Lucasium stenodactylum Oliver et al., 2007

MATERIAL EXAMINED

[*Diplodactylus polyophthalmus* (part.)] Günther, A. (1867). Paralectotype – unnumbered specimen in the collection of NHMUK from Nickol Bay (Karratha), Western Australia.

Holotype

Australia: Western Australia: WAM R14370 (juvenile), from Strelley River, Pilbara Division, Western Australia, collected by J.B. Cleland, probably August–October 1907; previously registered as 9876 on 27 March 1909 (see Ellis et al. 2018). The juvenile specimen is in very poor condition (Figure 1 in Ellis et al. [2018]).

See Appendix for additional material examined.

DIAGNOSIS

A *Lucasium* distinguished from other members of the genus by rostral excluded from nostril, rostral crease present, terminal apical plates slightly wider than width of the digits, tail moderately long (TailL%SVL ~0.77), males with 2–5 precloacal pores and females with 0–2 pores (usually none) and males with an enlarged cloacal spur typically flanked by a second smaller spur. Background colour rich reddish-brown, overlain by a network of dark variegations, small to medium pale yellowish spots scattered over dorsum; pale vertebral stripe typically absent, but if present usually poorly-defined.

DESCRIPTION

Body cylindrical with flat venter; head triangular, narrowing to rounded snout tip; eyes large; loreal region concave; moderate adductor muscles; ear opening small and circular; limbs gracile; five fingers and toes; tail long and tapering to fine point.

Rostral rectangular with crease extending from dorsal edge; rostral separated from nostril; two enlarged supranasals with rounded edges in narrow contact or separated by an internasal; enlarged upper and lower labials, approximately twice as wide as high; first supralabial approximately twice the height of second; scales on snout slightly enlarged; a small row of supraciliary spines in posterodorsal corner of the eye; mental with concave sides, flanked by three relatively large infralabials to each side, decreasing in size posteriorly (Figure 5B); gular scales decreasing in size, becoming granular on throat.

Scales on dorsum juxtaposed, rounded and slightly raised posteriorly; scales on venter juxtaposed and slightly rounded; scales on tail square and flattened, occurring in regular rows; in males a single large cloacal spur usually flanked by a second spur half to equal the size of the larger one on each side of tail base; precloacal pores dimorphic: 2–5 in mature males, typically 0 in females but occasionally up to 2; digits covered in fine scales, subdigital scales slightly enlarged; digits only slightly narrowing towards claw; paired terminal apical plates comparatively very wide, extending past margins of digit.

Pattern and colour. In life (Figures 6C, D), background colour rich reddish brown, with dark variegations tending to form a defuse network; vertebral stripe variably present, formed by connection of blotches or with wavy edges, stripe frequently completely absent; small to medium pale yellow spots scattered across dorsum; a more diffuse yellow colouration frequently encloses several small spots to form larger irregularly-shaped blotches; top of head with irregular defuse pale blotches; pale canthal stripe present, ventral edge with dark border; margins of eyelid highlighted with sulphur or yellow; tail pattern a continuation of body pattern, breaking into blotches distally. In preservative, specimens fade to a reddish-brown with most of the yellow hues lost (cf. Figures 6 vs. 7).

HABITAT

Occurs on a range of substrates, including red sandhills, loamy soils, stony ground, creek lines, gibber plains and claypans (see Figures 9C, D). In the Pilbara Biodiversity Survey, habitat variables associated with this species indicated an affiliation with sandy and loamy surfaces, and rugged surfaces at the lower edges of slopes (Doughty et al. 2011). Vegetation includes spinifex, acacia and eucalyptus. Shelters under low rocks, fallen logs and recorded from spider burrows.

DISTRIBUTION

This species is largely confined to the Pilbara region in Western Australia. It extends south along the coast to the North West Cape to the Gascoyne region as far as inland of Shark Bay and south-east to Kumarina (Figure 2). It is known from Barrow Island and the South Murion islands. In the sandy deserts to the north and east it is replaced by *L. stenodactylus*, and to the south-east by *L. bungabinna*.

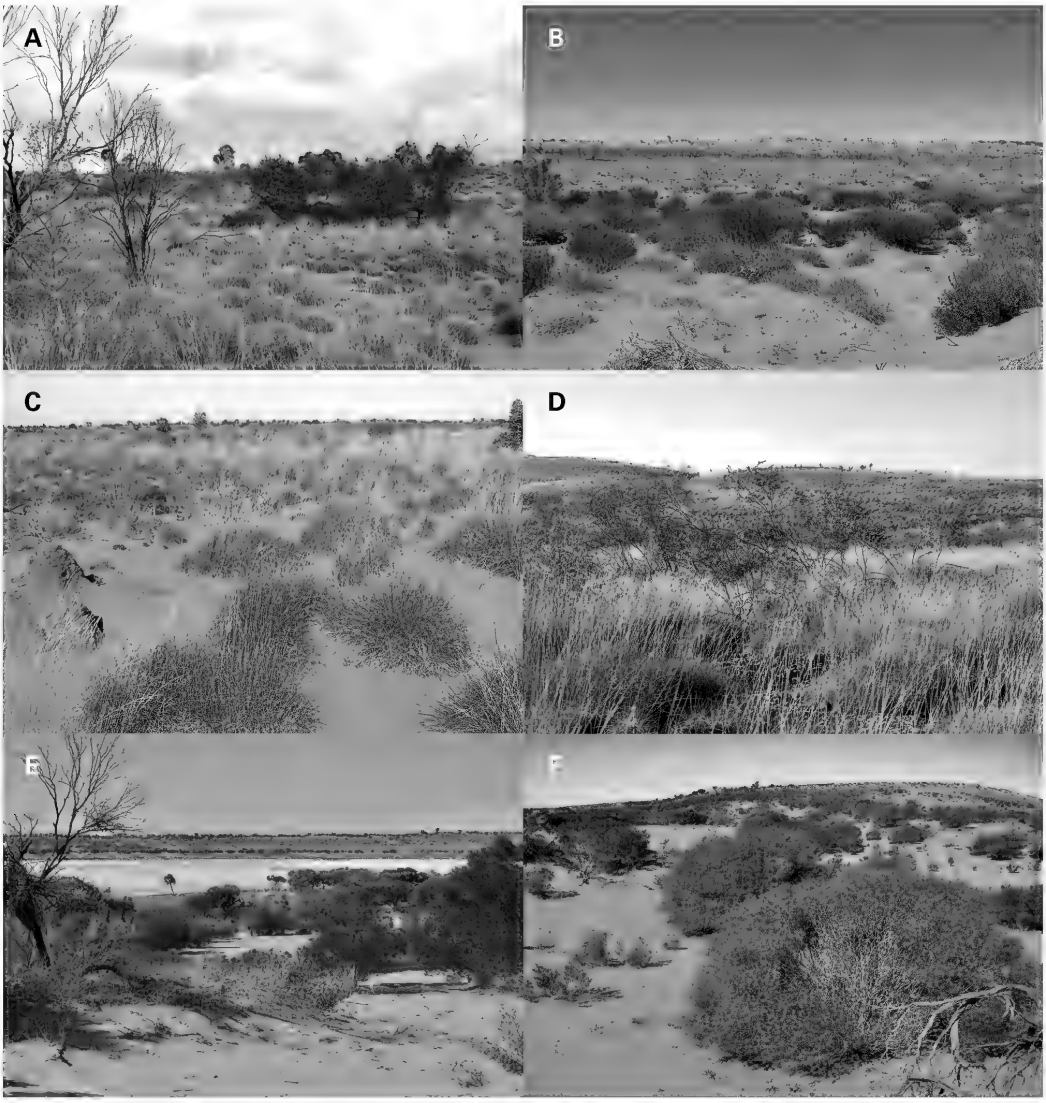

FIGURE 9 Habitats of lineages of the *Lucasium stenodactylus* species complex. A) Northern lineage, 30km W. Ilkurlka, Western Australia; B) Northern lineage, near Plumridge Lakes, Western Australia; C) Pilbara lineage, 50km E. Port Hedland, Western Australia; D) Pilbara lineage, 60km S. Karratha, Western Australia; E) South Australian lineage, near Lake Mary, South Australia; F) South Australian lineage, near Roxby Downs, South Australia. (Images A–D: B. Bush; E–F: M. Newton.)

COMPARISON WITH OTHER SPECIES

This species is most similar to *L. stenodactylus*, its sister species (Figure 1). Accordingly, many of the characters that separate *L. stenodactylus* from other *Lucasium* also separate *L. woodwardi* from them (see account above). These characters include homogeneous dorsal scales of similar size to those on venter, nostril separated from rostral and multiple precloacal pores.

The main morphological character that reliably separates *L. woodwardi* from *L. stenodactylus* is the size and shape of the terminal apical plates. These pads are larger in *L. woodwardi* and have greater medial contact proximally before angling outwards past the edge of the digit. In contrast, the pads in *L. stenodactylus* are much smaller and do not typically protrude past the digit, the pads are in narrow contact proximally before angling outwards to form a butterfly shape (see Figure 3).

Pattern and colouration also separate these two species, but there is some degree of overlap. *Lucasium woodwardi* has a much richer reddish-brown background colouration compared to *L. stenodactylus*, which has a much lighter appearance (Figure 6). Presence of a vertebral stripe is variable in *L. woodwardi*, but when present it typically has irregular or wavy edges. In contrast, *L. stenodactylus* from the western deserts has a strongly-defined straight-edged vertebral stripe. Where these two species meet at the edge of the northern and eastern Pilbara the contrast between them is strong. However, Kimberley and some Northern Territory *L. stenodactylus* have a tendency to have a less pronounced vertebral stripe and the more amoeboid pattern of irregular blotches that is more common in *L. woodwardi*, making identification of museum specimens of unknown locality difficult on pattern alone.

REMARKS

The close phenotypic resemblance of *L. woodwardi* and *L. stenodactylus* was reflected in the genetic results of Pepper et al. (2006, 2008) who found them to be sister taxa that diverged from each other ~5 mya. In his revision, Kluge (1967) barely commented on *L. woodwardi*, believing it to be *L. stenodactylus*. Not helping matters was the particularly poor state of the type specimen of *L. woodwardi*, a highly desiccated subadult, and the widely distributed '*D. stenodactylus* group' specimens that he examined over many years that were collected over a massive area of Australia (including those of the South Australian clade, his 'population B'). Owing to their ephemeral colours and often poor state of preservation in museum collections, the task of sorting large series of specimens into meaningful groups on the basis of colour pattern can be difficult, a problem that would have been more pronounced in the 1960s before specimens were preserved with the limbs and digits laid out and digital photographs taken.

Within the Pilbara, Pepper et al. (2008) found evidence for several major lineages within *L. woodwardi* that diverged from each other ~3–4.5 mya. They hypothesised that lineages may be adapted to different substrates within the region, but this has yet to be tested against a non-adaptive biogeographic diffusion hypothesis.

***Lucasium microplax* sp. nov.**

Southern sandplain gecko

Figures 3–7, 10

urn:lsid:zoobank.org:act:5A1388B2-86B6-4059-8209-3C697DE04AB4

MATERIAL EXAMINED

Holotype

Australia: ***South Australia*:** SAMA R48940, male, collected by G. Medlin and H. Ehmann from 6.4 km south-east of Stonewall Dam, Andamooka Station (30.7411°S, 137.3411°E) on 11 November 1996.

Paratypes

Australia: ***South Australia*:** SAMA R47644, male, Arcoona Station (31.074°S, 137.07°E); SAMA R50285, male, 3 km E Gap Well, Beltana Station (30.7844°S, 138.1547°E); SAMA R57229, male, Lake Beviss Paddock, Oakden Hills Station (31.5997°S, 136.7886°E); SAMA R57910, female, 59 km west-north-west of Emu (28.5367°S, 131.6067°E); SAMA R59337, male, 41 km north-north-west of Maralinga (29.8964°S, 131.2792°E).

Australia: ***Western Australia*:** WAM R166307, female, 16.8 km east-north-east of Blackstone (25.935°S, 128.438°E).

Australia: Northern Territory: NTM R25650, male, 10 km south of Kulgera (25°55'S, 133°12'E).

See Appendix for additional material examined.

DIAGNOSIS

A *Lucasium* distinguished from other members of the genus by rostral in point contact with nostril, rostral crease present, terminal apical plates very small, not extending past digits, tail relatively short (TailL%SVL ~0.70), males and females with two precloacal pores and males with two enlarged cloacal spurs. Background colour a plain dark reddish-brown, isolated small to medium pale yellowish spots on sides that may be connected to well-defined vertebral stripe narrowly outlined by black.

DESCRIPTION

Body cylindrical with flat venter; head triangular, narrowing to rounded snout tip; eyes large; loreal region concave; moderate adductor muscles; ear opening small and oval shaped; limbs gracile; five fingers and toes; tail long and tapering to fine point.

Rostral rectangular with crease extending to 1/3 into scale from dorsal edge; rostral usually in point contact

with nostril, at most, narrowly excluded from nostril; two enlarged supranasals with rounded edges always in narrow to moderate contact; enlarged upper and lower labials, approximately twice as wide as high; first supralabial 1.5 times the height of second; scales on snout slightly enlarged; several spinose scales on posterior edge of eyebrow; mental elongate, over twice the length as width, flanked by three large infralabials on each side, decreasing in size posteriorly, all infralabials relatively elongate (Figure 5C); gular scales decreasing in size, becoming granular on throat.

Scales on body juxtaposed, rounded and slightly raised posteriorly; scales on venter juxtaposed and slightly rounded; two enlarged cloacal spurs on each side of tail; precloacal pores in males and females 2, rarely 0; scales on tail square and flattened, occurring in regular rows; digits covered in fine scales, subdigital scales slightly enlarged; digits noticeably narrowing towards claw on distal phalanx; paired terminal apical plates very small, not extending past edges of digit.

Pattern and colour. In life, background colour dark reddish brown; pale beige vertebral stripe with straight well-defined edges; vertebral stripe forks at neck, continuing anteriorly above and through eye, continuing along canthus as pale streak to tip; top of head with irregular defuse pale blotches; margins of eyelid highlighted with sulphur or yellow pigmentation; on lateral surfaces of body, a simple pattern of moderately large pale yellow spots contrasting with background colouration; yellow spots variably connected to vertebral stripe or neighbouring spots; blotches occasionally forming a lateral line on forebody, extending below ear and connecting with gular region; dorsal surface of digits whitish; dorsal region of tail with a series of pale blotches; ventral surfaces drab white. In preservative, background colour becomes dark brown and yellow hues entirely lost.

Measurements of holotype (in mm). SVL – 51.5; TrunkL – 25.4; TailL – 31.5 (regenerated); TailW – 3.8; ArmL – 6.8; LegL – 8.6; HeadL – 13.6; HeadW – 8.4; HeadH – 5.6; OrbL – 3.5; NarEye – 4.7; SnEye – 5.3; EyeEar – 3.8; INar – 1.8; IO – 3.6; SupLab – 10; InfLab – 10; CreaseL – 15%; AntSup – 5; MenL – 1.4; MenL/W – 1.34; Pores – 2; Tail%SVL – 61.2 (regenerated); HeadL/SVL – 0.26; HeadW/SVL – 0.16; HeadH/SVL – 0.11.

HABITAT

This species occurs on a range of substrates, from compact sand, to coarse sand to sandy clay and stony country. In contrast, it is not known to occur on gibber, cracking clay or soft dune sand.

DISTRIBUTION

Most specimen records are from South Australia (Figure 2). In Western Australia, known from Blackstone and Warburton near the South Australia-Northern Territory border. Occurs in the central southern Northern Territory as far north as the Barrow Creek area. In Queensland it occurs in the Simpson

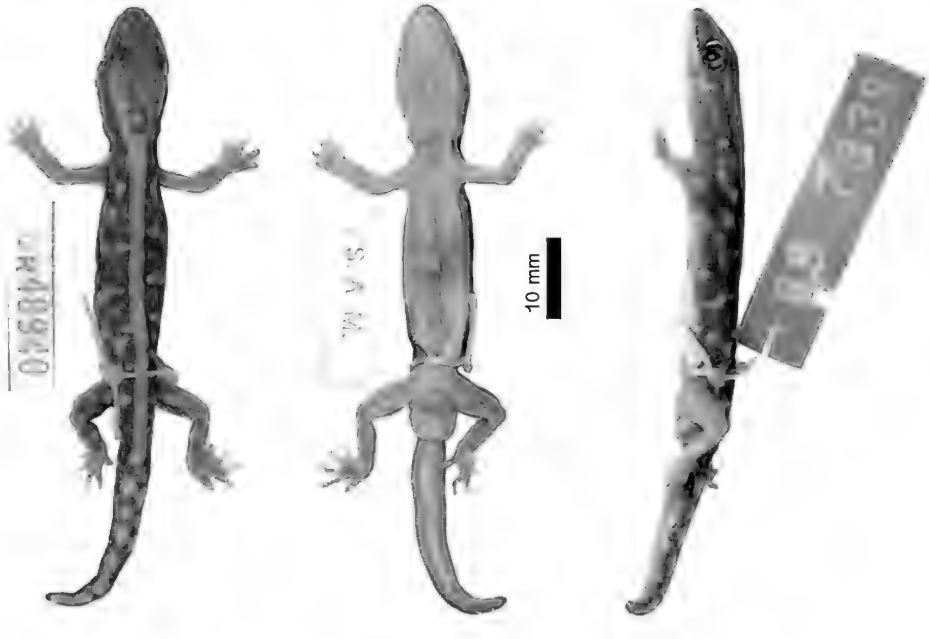

FIGURE 10 Holotype of *Lucasium microplax* sp. nov. in dorsal, ventral and lateral views. Scale bar = 1 cm.

desert in the south-west corner near the Northern Territory, as far east as Welford National Park and south to Bullo Downs. In New South Wales they occur in the extreme north-west of the state, with records from Sturt National Park, Milparinka and Thurloo Downs.

ETYMOLOGY

The specific name *microplax* means 'small plate' (Greek), in reference to the tiny apical plates in this species. Used as a noun in apposition.

COMPARISON WITH OTHER SPECIES

Lucasium microplax can be separated from its congeners on several scalation and pattern elements. It possesses homogeneous dorsal and ventral scales of approximately the same size compared to *L. byrnei* (heterogeneous dorsals) and *L. squarrosum* (enlarged dorsals). Males and females almost always have two precloacal pores (one on each side) in contrast to those species with more than two (*L. stenodactylus*, *L. woodwardi*) or zero (*L. byrnei*, *L. maini*, *L. occultum* and *L. steindachneri*). In *L. microplax*, the rostral is in point contact with the nostril most of the time (Figure 4B), although this varies occasionally with more extensive contact or narrow separation among individuals and is best used in combination with other characters.

Based on the presence of a strong vertebral stripe with straight edges, *L. microplax* resembles *L. stenodactylus*, *L. bungabinna* and *L. immaculatum* most, but differs in scalation and subtle elements of pattern and colouration. The new species possesses tiny apical plates, whereas *L. bungabinna* and *L. immaculatum* have much larger terminal lamellae. From *L. stenodactylus*, it differs by having the rostral and nostril in point contact, two precloacal pores, much smaller apical plates on a narrow terminal phalanx and a shorter tail. The pattern of the new species also has a more uniform dark brown background compared to the lighter *L. stenodactylus*, with the spots larger and in higher contrast.

REMARKS

After over 50 years since Kluge (1967) first posited that *L. microplax* (as his 'population B') could represent a new species, the molecular evidence of Pepper et al. (2006) and this study, coupled with a detailed examination of specimens from the WAM and SAMA collections have resolved the morphological variation sufficiently to confirm Kluge's 'population B' as a new species.

The new species has an odd distribution, with its limits almost completely conforming to the borders of the state of South Australia. A detailed examination of specimens from across northern South Australia revealed no individuals of *L. stenodactylus*, while in south-western Northern Territory (Yulara, Curtin Springs) only *L. stenodactylus* has been recorded. Further field work in the states that adjoin northern South Australia would be useful in clarifying the geographic extent of each species, habitat preferences and the degree to which the two species contact or overlap. There is an area of overlap between *L. microplax* and *L. stenodactylus* in south-central Northern Territory but at present no syntopic locations are known.

The unusual degree to which the distributions of *L. stenodactylus* and *L. microplax* align with state borders potentially explains why it took some time for the existence of two species to be recognised. Since each Australian state or territory has its own museum collection and research institute, it is possible that previous workers relegated one or two odd-looking '*L. stenodactylus*' specimens in their collections to variation within that species. Only by drawing from specimens and tissue samples from several collections was it possible to demonstrate an abrupt and consistent change in both morphology and genetic data that has led to resolution of arid '*L. stenodactylus*'.

DISCUSSION

The taxonomy presented here further resolves ambiguity across the widespread *L. stenodactylus* species complex. The new species from South Australia had been suspected as early as the 1960s by Kluge (1967), but the species concepts employed then and with collections from the AAZ in their infancy, he simply denoted the Western Australian and South Australian populations in his monograph and did not formally describe them as separate species. Interestingly, he saw little evidence for recognising *L. woodwardi* from the Pilbara as a separate species from the western desert *L. stenodactylus* at the time. Again, this may have been due to critical lack of specimens available to him in the 1960s when collections had not yet grown owing to the development of the resource industry in the Pilbara. Equally, the introduction of molecular genetic methods has allowed us to overcome the problems posed by the extremely poor condition of the type of *Diplodactylus woodwardi*. By demonstrating the Strelley River type locality is occupied by a species that is distinct from *L. stenodactylus*, it has been possible to re-examine the type of *L. woodwardi* and to interpret its morphology with more confidence.

An unexpected insight of this study was that although long associated with *L. stenodactylus*, *L. microplax* is less closely related to that species than it is to some other *Lucasium*. Morphology within *Lucasium* appears to be an indifferent predictor of phylogenetic relationships, with morphologically distinctive species scattered among more conservatively patterned and structured species. Across *Lucasium*, there is a consistent colour pattern that is present in most species, comprising a reddish-brown dorsum patterned with numerous small pale spots and a vertebral stripe (sometimes broken into large semi-confluent blotches) that forks on the nape to terminate behind each eye, usually continuing as a canthal streak to the nostrils. Most species have adhesive terminal toe pads that are small to very small and

dorsal scales that are homogeneous and small. Species that diverge from one or more of these generalisations include *L. byrnei*, *L. wombeyi* and *L. alboguttatum* (colour pattern), *L. byrnei* and *L. squarrosum* (dorsal scalation), with the members of each of these subgroups not closely related to one another, and the padless *L. damaeum* is the sister of *L. alboguttatum* (toe pads moderately large) and *L. maini* (toe pads minute), not the very small-padded *L. squarrosum* or *L. microplax*.

Adaptive explanations of these morphological variations within *Lucasium* are hard to find. Most species are terrestrial and only climb, if at all, on very low vegetation (e.g. Oliver et al. 2008). The only rock-associated species, *L. wombeyi*, is perhaps the most divergent member of the genus in its slender, long-legged body form and relatively large adhesive pads, both consistent with moving over bare rock surfaces. However, the remaining species do not present much obvious adaptive correlation with substate or habits. Large, small or no toe pads are found in desert sand-dwelling species, while moderate to small toe pads are found on species living on arid loamy or clayey terrain. Further study of the species when they are active at night may help clarify the degree to which their foraging behaviour and choice of microhabitat might correlate with the degree of toe pad development.

Based on a rough but commonly used mean rate of 2% pairwise sequence divergence per million years for the ND2 locus (Zamudio and Greene 1997; Oliver et al. 2010), divergences between the members of *Lucasium* treated here (~11–19%) indicate speciation largely occurred during the late Miocene, roughly 5.5–9.5 mya. This timing is concordant with a deepening of aridity across the AAZ, and is consistent with major radiations within other gekkonid species groups (e.g. Pepper et al. 2011; Oliver et al. 2014; Brennan et al. 2016; Laver et al. 2017).

Much of the recent taxonomic and population genetic work on *Lucasium* has been a progressive increase in our understanding of what constitutes inter- and intraspecific variation, which has been marked by a steady reduction in the set of populations that should be included within '*L. stenodactylus*' as additional species are recognised. Our restriction of *L. stenodactylus* is a further step, but this problem is still a work in progress. The Australian monsoonal tropics, the west of Queensland and New South Wales, the southern limits of the Northern Territory and eastern Great Victoria Desert in Western Australia remain poorly sampled for members of this genus. Given the variation which exists within our restricted concept of *L. stenodactylus*, future studies may be necessary to complete the revision of this species.

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APPENDIX Specimens of *Lucasium* used in this study. 'Morphology' — used in morphological assessment; 'Genotyped' — used in genetic analyses (x - this study; P06 - Pepper et al. [2006]).

Taxon	Collection	Specimen number	Location	Latdec	Londec	Morphology	Genotyped	GenBank
Northern	NTM	R6299	8KM S. Katherine, NT	-14.4833	132.3333	x		
Northern	SAMA	R29878	25.4km NNW. Curtin Springs Homestead, NT	-25.1917	131.6167		x	MW324003
Northern	SAMA	R36111	Yulara Township, NT	-25.2333	131.0167		x	MW324007
Northern	WAM	R108382	Sunrise Hill, WA	-20.5000	120.0800	x		
Northern	WAM	R108803	19km NE. Sandfire Roadhouse, WA	-19.7000	121.2333	x		
Northern	WAM	R110591	Tanami Desert, WA	-19.8986	128.8658	x	P06	
Northern	WAM	R110615	Tanami Desert, WA	-19.8997	128.8270	x		
Northern	WAM	R110766	Jimblebar East, WA	-23.3861	120.2353	x		
Northern	WAM	R127163	Nifty Mine, WA	-21.6666	121.5833	x		
Northern	WAM	R157732	Tanami Desert, WA	-19.5794	128.8681	x		
Northern	WAM	R157733	Tanami Desert, WA	-19.5794	128.8681	x		
Northern	WAM	R157946	Lake Disappointment, WA	-23.2983	122.7017	x		
Northern	WAM	R157947	Lake Disappointment, north-western lake edge, WA	-23.2341	122.7014	x		
Northern	WAM	R157949	Lake Disappointment, WA	-23.2983	122.7017	x		
Northern	WAM	R166309	22.6km NE. Blackstone, WA	-25.8572	128.4456		x	MW324006
Northern	WAM	R166325	5.3km SSE. Pungkulpirri Waterhole, WA	-24.7072	128.7603		x	MW324005
Northern	WAM	R175154	Kiwirrkurra Remote Community, WA	-22.8123	127.8313	x		
Northern	WAM	R21407	4mi E. Tennant Ck, NT	-19.6500	134.2500	x		
Northern	WAM	R84551	15km NE. Mt Aloysius, WA	-25.8000	128.6000	x		
Northern	WAM	R94774	~80km S. Telfer, WA	-22.3247	122.0756	x		
Northern	WAM	R94775	~80km S. Telfer, WA	-22.3280	122.0842	x		
Pilbara	WAM	R102053	De Grey River, WA	-20.3166	119.2500	x	P06	
Pilbara	WAM	R106155	31.5km SSW. Turee Ck Homestead, WA	-23.8666	118.5667	x	P06	
Pilbara	WAM	R108835	Kumarina Roadhouse, WA	-24.7000	119.6000	x	P06	
Pilbara	WAM	R110130	8km S. Coolawanyah (PBS-PE02), WA	-21.8822	117.7950	x	P06	

Taxon	Collection	Specimen number	Location	Latdec	Londec	Morphology	Genotyped	GenBank
Pilbara	WAM	R111806	16.8km SW. Pannawonica (PBS-BDRS02), WA	-21.7594	116.2275	x		
Pilbara	WAM	R111815	36km E. Wheelarra Hill (PBS-BDRS02), WA	-23.3831	120.4790	x		
Pilbara	WAM	R111843	14km SE. Wheelarra Hill (PBS-BDRS10), WA	-23.4711	120.2150	x		
Pilbara	WAM	R111858	22km SE. Wheelarra Hill (PBS-BDRS11), WA	-23.4986	120.2910	x		
Pilbara	WAM	R113031	Lesley Salt Works, WA	-20.2472	118.8472	x	P06	
Pilbara	WAM	R113591	42km NNE. Auski Roadhouse, WA	-21.9233	118.8333	x	P06	
Pilbara	WAM	R114920	6km E. Marble Bar, WA	-21.1666	119.8167	x	P06	
Pilbara	WAM	R115245	South Muiron Islands, WA	-21.6333	114.3833	x	P06	
Pilbara	WAM	R127703	5km S. Mt Tom Price, WA	-22.7991	117.7764	x	P06	
Pilbara	WAM	R132239	Urala Station, WA	-21.7777	114.8706	x	P06	
Pilbara	WAM	R154560	Wheelarra Hill, WA	-23.3791	120.1053	x	P06	
Pilbara	WAM	R156157	Waldburg Station, WA	-24.7811	116.9589	x	P06	
Pilbara	WAM	R158319	3.8km N. Giralia Homestead, WA	-22.6577	114.3919	x	P06	
Pilbara	WAM	R161075	7km SE. Marda Pool (PBS-DRW09), WA	-21.0699	116.2070	x	P06	
Pilbara	WAM	R161101	7.7km SW. Yanyare River Mouth (PBS-DRW03), WA	-20.8514	116.3770	x		
Pilbara	WAM	R161152	14km WSW. Roy Hill Station (PBS-RHNE05), WA	-22.6757	119.8410	x		
Pilbara	WAM	R170180	46km WSW. Tom Price (PBS-TCMBW01), WA	-22.8261	117.3710	x		
Pilbara	WAM	R170184	46km WSW. Tom Price (PBS-TCMBW01), WA	-22.8261	117.3710	x		
Pilbara	WAM	R170213	45km WSW. Tom Price (PBS-TCMBW02), WA	-22.8347	117.3820	x		
Pilbara	WAM	R170253	31km SE. Paraburdoo (PBS-TCMBC07), WA	-23.4164	117.8690	x		
Pilbara	WAM	R170264	51km ESE. Paraburdoo (PBS-TCMBC12), WA	-23.2925	118.1560	x		
Pilbara	WAM	R170272	19km SSW. Paraburdoo (PBS-TCMBC01), WA	-23.3644	117.6250	x		
Pilbara	WAM	R90635	Woodstock Station, WA	-21.6094	118.9744	x		
Pilbara	WAM	R90671	Woodstock Station, WA	-21.6094	118.9744	x		
SA	NTM	R14338	6km SSW. Claraville, NT	-23.4170	134.7340		x	MW323969
SA	NTM	R25650	10km S. Kulgera, NT	-25.9167	133.2000	x		
SA	SAMA	R20899	Olympic Dam, Roxby Downs, SA	-30.3800	136.8800		x	MW323993

Taxon	Collection	Specimen number	Location	Latdec	Londec	Morphology	Genotyped	GenBank
SA	SAMA	R26234	10km N. Lake Phillipson	-29.3583	134.4700		x	MW323994
SA	SAMA	R26536	Granite Downs Station, SA	-26.9500	133.5700		x	MW323968
SA	SAMA	R31828	23km SE. Lake Bring, SA	-30.3186	133.2161		x	MW323995
SA	SAMA	R32310	Lyons Siding, SA	-30.6300	133.9300		x	MW324002
SA	SAMA	R40901	Carmeena Well area, SA	-27.1331	132.4239		x	MW323984
SA	SAMA	R41864	6.8km S. Blue Hills Bore, SA	-27.1944	132.8686		x	MW323970
SA	SAMA	R42516	2km SE. Tallaringa Well, SA	-29.0500	133.3200		x	MW323960
SA	SAMA	R44897	1.5km ENE. Dulkaninna, SA	-28.9350	138.6178		x	MW323971
SA	SAMA	R45122	Yalymboo Paddock, Yalymboo Station, SA	-31.5422	136.6764		x	MW323996
SA	SAMA	R45290	Mt Vivian Station, 1.35km SE Crows Nest Bore, SA	-30.8422	135.7400		x	MW323997
SA	SAMA	R46380	2.4km E. Kenneberry Waterhole, SA	-29.6381	137.8078		x	MW323973
SA	SAMA	R46431	18.3km SW. Backadinna Hill, SA	-29.2889	135.1833		x	MW323975
SA	SAMA	R46454	3.5km NW. Beresford Rail Station, SA	-29.2164	136.6308		x	MW323972
SA	SAMA	R46493	7.6km NW. Mungutana Dam, SA	-29.2714	135.6328		x	MW323974
SA	SAMA	R46808	3.2km N. Anvil Hole Native Well, Witjira, SA	-26.3292	135.7053		x	MW323976
SA	SAMA	R47229	6.3km SSW. Ninety Nine Dam, Anna Ck Station, SA	-28.9508	136.7819		x	MW323977
SA	SAMA	R47289	8.4km NE. Mussel W/H, Peake Station, SA	-28.4156	136.4464		x	MW323978
SA	SAMA	R47317	6.5km ESE. Coppertop Hill, Peake Station, SA	-28.1453	136.0281		x	MW323979
SA	SAMA	R47450	1.2km SSW. Oolarinna East Bore, SA	-27.6250	132.9119		x	MW323988
SA	SAMA	R47641	Near Sangsters Bore, Todmorden Station, SA	-27.0700	134.8200		x	MW323998
SA	SAMA	R47644	Arcoona Station, SA	-31.0700	137.0700	x	x	MW323999
SA	SAMA	R48443	2.4km W. Little Cadna-owie Spring, Allandale Station, SA	-27.7861	135.6592		x	MW323980
SA	SAMA	R48543	1km SE. Muntee Kullana Bore, Macumba Statoin, SA	-27.7458	136.6994		x	MW323981
SA	SAMA	R48683	Kokatha Station, SA	-31.4092	135.3514		x	MW324000
SA	SAMA	R48940	6.4km SE. Stonewall Dam, Andamooka Station, SA	-30.7411	137.3411	x	x	MW323982
SA	SAMA	R50118	2.7km WSW. Sentinel Hill, SA	-26.1019	132.4353	x		
SA	SAMA	R50166	3.2km WNW. Sentinel Hill, SA	-26.0728	132.4192	x	x	MW323989

Taxon	Collection	Specimen number	Location	Latdec	Londec	Morphology	Genotyped	GenBank
SA	SAMA	R50285	3km E. Gap Well, Beltana Station, SA	-30.7844	138.1547	x		
SA	SAMA	R50286	3km E. Gap Well, Beltana Station, SA	-30.7844	138.1547	x		
SA	SAMA	R51218	22.9km WSW. Mundy Dam, SA	-26.5544	132.8672	x	x	MW323990
SA	SAMA	R51576	35km ESE. Amata, SA	-26.2769	131.4606	x	x	MW323991
SA	SAMA	R51620	29.2km ENE. Mimili, SA	-26.8975	132.9753	x		
SA	SAMA	R51622	29.7km WNW. Indulkana, SA	-26.8744	133.0272	x	x	MW323992
SA	SAMA	R52477	5km E. Woocalla, south of Pernatty Lagoon, SA	-31.6903	137.2442		x	MW324001
SA	SAMA	R52779	11.7km SSW. Mount Sarah homestead, SA	-27.0256	135.2211		x	MW323985
SA	SAMA	R52812	19.4km ESE. Oolgaawa W/H, SA	-26.8347	136.0717		x	MW323986
SA	SAMA	R53061	20km SE. Leigh Creek Town, SA	-30.4681	138.2808	x	x	MW323983
SA	SAMA	R54126	28.8km NW. Muloorina homestead, SA	-29.0786	137.6714		x	MW323987
SA	SAMA	R56454	5.6km W. Mt Hoare, SA	-27.0575	129.6439	x	x	MW323966
SA	SAMA	R57229	28km E. Vokes Hill Corner, SA	-28.5619	131.0014	x		
SA	SAMA	R57910	59km WNW. Emu, SA	-28.5367	131.6067	x		
SA	SAMA	R57911	59km WNW. Emu, SA	-28.5367	131.6067	x		
SA	SAMA	R57931	44.7km ESE. Emu, SA	-28.8525	132.5858	x		
SA	SAMA	R57945	51.1km ESE. Emu, SA	-28.8628	132.6556	x		
SA	SAMA	R58047	25km NE. Half Moon Lake, SA	-29.8761	133.6181		x	MW323961
SA	SAMA	R58973	47.4km W. Oak Valley, SA	-29.5086	130.2550	x	x	MW323967
SA	SAMA	R59337	41km NNW. Maralinga, SA	-29.8963	131.2791	x	x	MW323962
SA	SAMA	R59481	67.1km NNW. Maralinga, SA	-29.7325	131.0858	x	x	MW323963
SA	SAMA	R59484	67.1km NNW. Maralinga, SA	-29.7325	131.0858	x		
SA	SAMA	R60538	26.8km SSW. Mt Dare, SA	-26.3022	135.1783		x	MW323964
SA	WAM	R166307	16.8km ENE. Blackstone, WA	-25.9352	128.4378	x		
SA	WAM	R166308	16.8km ENE. Blackstone, WA	-25.9352	128.4378		x	MW323965
SA	WAM	R77991	23km NE. Warburton, WA	-26.0000	126.7500		P06	
SA	WAM	R77992	23km NE. Warburton, WA	-26.0000	126.7500		P06	